# STUDIES IN MILK SECRETION. V. ON THE VARIATIONS AND CORRELATIONS OF MILK SECRETION WITH AGE[1]

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## INTRODUCTION

A large body of exact scientific data on milk production has been accumulated since the time of the establishment of the ADVANCED REGISTRY SYSTEM of the HOLSTEIN-FRIESIAN ASSOCIATION OF AMERICA and its later adoption by the Associations of the other breeds of dairy cattle. These completed records are unique in several ways, chief among which

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is the fact that the records of the cows included among them must meet a certain standard of performance. This standard for entry has the effect of cutting out certain records of cows of the given breed. Thus the JERSEY REGISTRY OF MERIT (THE AMERICAN JERSEY CATTLE CLUB 1906) says that, "if the test is commenced the day the cow is two years old, or previous to that day, she must produce within one year from the date the test begins, 250.5 pounds of butter-fat. For each day the cow is over two years at the beginning of her year's test, the amount of butter-fat she must produce in the year is fixed by adding 0.1 (one-tenth) of a pound for each such day to the 250.5 pounds required when two years old. This ratio of increase applies until the cow is five years old at the beginning of her test, when the required amount will have reached 360 pounds, which will be the amount of butter-fat required of all cows five years old or over. These standards are based upon one complete year's record from the time of beginning, regardless of any time which may be lost by being dry or calving during the period." Three facts are obviously true of the JERSEY REGISTRY OF MERIT cows as compared with a true sample taken at random of the milking cows of the Jersey breed; (1) the cows making up the REGISTRY OF MERIT are a selected sample; (2) the scale of the selection is linear having its lower limit 250.5 pounds of butter-fat production at 2 years and its upper limit 360 pounds at 5 years and over; (3) this requirement means that for each day of age at test that frequency distributions of years production are cut off perpendicularly at the requirement and only those animals making greater yields than this are allowed to be entered into the REGISTRY OF MERIT. The data taken from this REGISTRY OF MERIT are not the true data for the Jersey breed and conclusions based on it cannot be considered as applying to the breed as a whole or to the general problems of milk secretion.

## MATERIAL AND METHODS

To supply this need of exact data on the Jersey breed as a whole the MAINE AGRICULTURAL EXPERIMENT STATION has obtained the recorded data on one of the largest pure-bred Jersey herds known. The data are exceptional in the following ways: (1) The records extend back to the year 1897 when the herd was organized; (2) the animals are practically all straight Island stock: (3) they have been under the oversight and direction of one manager since 1901; (4) exact records are kept of the milk production, butter fat and butter-fat percent; (5) many of the individual animals have records for several different lactations. The elimi-

nation of variation of the milk production of cows or groups of cows caused by changes of any one or more of these five factors is important for the analysis of the causative mechanism of milk and butter-fat production. It is obvious that these records are free from such variables. They constitute a homogeneous group of data representing the Island Jersey under constant conditions of management and climate.

Such an accumulation of exact statistical data on the cows of the Jersey breed for problems of so much interest, both biologically and economically, warrants the application of adequate biometrical methods in their analysis. Such analysis is now well recognized by most investigators as of the utmost importance to our understanding of the fundamental principles of physiology which underlie the process of milk secretion itself.

The general problems attacked are those of the individual variation between the lactating functions of different dairy cows at a given age. What is the true type of the frequency distributions of milk production? What relation exists between the mean productions of the successive ages in a true random sample of the Jersey breed? An understanding of these and similar questions is necessary to the fuller utilization of the data found in the herd book of the registry association for as previously pointed out the requirement for entrance acts as a true truncating agent to the frequency distribution of a given age. Without a knowledge of the type of these frequencies no true correction factors may be determined to properly allow for the increase in age of the cows either for direct comparison of yields or for inheritance studies.

The biometrical methods used are in general those of any adequate analytical treatment of a quantitative subject. In each case reference to the source of the original publication where the methods may be found are given where the formula is first used. In each case the standard deviations have SHEPPARD's correction applied to them as a glance at the data shows that high contact is present in the distributions.

The data used for study are all from normal, healthy cows. Two diseases have been present in the herd, tuberculosis and abortion. The tuberculous animals were all eliminated early in the herd's history by the use of the tuberculin test. All records from animals which were proven to be tubercular or which aborted were not used. Records from animals normally healthy but sick during a given lactation were not used. All of the cows have been kept in climatic conditions similar to those of western Virginia.

A word as to the method of keeping the data and its transfer to this

STATION is perhaps necessary. All records are made at the time of milking on the daily milk sheets for the given cow which are kept in the barn. The milking takes place twice a day, the records are for night and morning. The weekly production taken from these sheets is transferred to the herd ledger by a trained bookkeeper. The total production for a given month is found together with the yearly production by adding the weekly totals. All records are recorded to pounds and tenths. The cows are tested bi-monthly by the BABCOCK test and the percentage of butter-fat is recorded beside its corresponding monthly milk yield. All weighings and readings are recorded immediately after they are made so there is little chance of inaccuracy. From these records the author has extracted 1741 complete 8-months records of healthy cows for milk production. Of these 1741, 1713 have records for the butter-fat percent. The weighted monthly averages of the bi-monthly test have been used to obtain the weighted 8-months average for the 8-months lactation period chosen for study.

## VARIATION OF JERSEY MILK PRODUCTION WITH AGE AT COMMENCEMENT OF TEST

The tabulation of these records in complete eight-months records has been done by the author. The choice of a proper interval of grouping for age was decided upon as one year, that is, grouping all of those records commenced while the cows were 2 years, no months and no days, to 3 years, no months and no days, and so on to include up to 10 years, no months and no days. The group 10 years-and-above has been included in one group as the numbers were quite small in the older age classes. The absolute and percentage frequencies determined for the different age classes are shown in table 1.

Table 1 together with figure 1 makes clear the following points in regard to frequency distributions of milk production.

(1) The frequency polygons show milk production to be quite symmetrical.

(2) The range of variation is quite considerable, extending from one cow which produced under 1500 pounds for the eight-months period to one which produced over 10,000 pounds.

(3) The polygons change their shape with increase in age at the commencement of the test, those of the early ages being higher at the mode and less scattered than those of the later years.

(4) There appears to be only one mode in all of the distributions. From this it seems probable that the polygons belong to the unimodal

TABLE I

*Frequency distributions of variations for the eight-months lactation records of a homogeneous herd of Jersey cows at different ages. Absolute and percentage frequencies.*

| Pounds of milk produced | Age, 2 yrs., 0 mos., to 3 yrs., 0 mos. | | Age, 3 yrs., 0 mos., to 4 yrs., 0 mos. | | Age, 4 yrs., 0 mos., to 5 yrs., 0 mos. | | Age, 5 yrs., 0 mos., to 6 yrs., 0 mos. | | Age, 6 yrs., 0 mos., to 7 yrs., 0 mos. | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Absolute frequency | Percentage frequency | Absolute frequency | Percentage frequency | Absolute frequency | Percentage frequency | Absolute frequency | Percentage frequency | Absolute frequency | Percentage frequency |
| 1000 to 1500 | 1 | .3 | | | | | | | | |
| 1500 to 2000 | | | | | | | | | | |
| 2000 to 2500 | 5 | 1.6 | 3 | 1.2 | | | | | | |
| 2500 to 3000 | 23 | 7.6 | 7 | 2.8 | 2 | .8 | | | 2 | 1.0 |
| 3000 to 3500 | 60 | 19.7 | 27 | 10.7 | 15 | 6.1 | 12 | 5.4 | 6 | 3.1 |
| 3500 to 4000 | 58 | 19.1 | 31 | 12.3 | 26 | 10.5 | 26 | 11.7 | 16 | 8.3 |
| 4000 to 4500 | 67 | 22.0 | 47 | 18.7 | 44 | 17.8 | 28 | 12.6 | 23 | 12.0 |
| 4500 to 5000 | 54 | 17.8 | 49 | 19.4 | 44 | 17.8 | 33 | 14.8 | 23 | 12.0 |
| 5000 to 5500 | 23 | 7.6 | 36 | 14.3 | 49 | 19.8 | 40 | 17.9 | 29 | 15.1 |
| 5500 to 6000 | 11 | 3.6 | 21 | 8.3 | 28 | 11.3 | 25 | 11.2 | 24 | 12.5 |
| 6000 to 6500 | 2 | .7 | 15 | 6.0 | 15 | 6.1 | 19 | 8.5 | 28 | 14.6 |
| 6500 to 7000 | | | 6 | 2.4 | 11 | 4.5 | 16 | 7.2 | 13 | 6.8 |
| 7000 to 7500 | | | 7 | 2.8 | 6 | 2.4 | 13 | 5.8 | 13 | 6.8 |
| 7500 to 8000 | | | 2 | .8 | 5 | 2.0 | 5 | 2.2 | 7 | 3.6 |
| 8000 to 8500 | | | 1 | .4 | 1 | .4 | 4 | 1.8 | 4 | 2.1 |
| 8500 to 9000 | | | | | 1 | .4 | 1 | .4 | 2 | 1.0 |
| 9000 to 9500 | | | | | | | | | 1 | .5 |
| 9500 to 10000 | | | | | | | | | 1 | .5 |
| 10000 to 10500 | | | | | | | 1 | .4 | | |
| Total | 304 | 100.0 | 252 | 100.1 | 247 | 99.9 | 223 | 99.9 | 192 | 99.9 |

TABLE I (continued)

*Frequency distributions of variations for the eight-months lactation record of a homogeneous herd of Jersey cows at different ages. Absolute and percentage frequencies.*

| Pounds of milk produced | Age, 7 yrs., 0 mos., to 8 yrs., 0 mos. | | Age, 8 yrs., 0 mos., to 9 yrs., 0 mos. | | Age, 9 yrs., 0 mos., to 10 yrs., 0 mos. | | Age, 10 yrs., 0 mos., to above | | Total population | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Absolute frequency | Percentage frequency | Absolute frequency | Percentage frequency | Absolute frequency | Percentage frequency | Absolute frequency | Percentage frequency | Absolute frequency | Percentage frequency |
| 1000 to 1500 | | | | | | | | | 1 | .1 |
| 1500 to 2000 | | | | | | | | | | |
| 2000 to 2500 | 2 | 1.2 | | | 2 | 2.4 | 1 | .9 | 13 | .7 |
| 2500 to 3000 | 1 | .6 | 1 | .8 | 6 | 7.1 | 3 | 2.8 | 50 | 2.9 |
| 3000 to 3500 | 7 | 4.1 | 9 | 7.1 | 5 | 5.9 | 10 | 9.3 | 166 | 9.5 |
| 3500 to 4000 | 16 | 9.4 | 15 | 11.8 | 6 | 7.1 | 8 | 7.5 | 212 | 12.2 |
| 4000 to 4500 | 24 | 14.1 | 15 | 11.8 | 11 | 12.9 | 18 | 16.8 | 279 | 16.0 |
| 4500 to 5000 | 20 | 11.8 | 13 | 10.2 | 15 | 17.6 | 21 | 19.6 | 274 | 15.7 |
| 5000 to 5500 | 28 | 16.5 | 27 | 21.3 | 15 | 17.6 | 19 | 17.8 | 266 | 15.3 |
| 5500 to 6000 | 21 | 12.4 | 15 | 11.8 | 5 | 5.9 | 12 | 11.2 | 162 | 9.3 |
| 6000 to 6500 | 20 | 11.8 | 13 | 10.2 | 8 | 9.4 | 7 | 6.5 | 127 | 7.3 |
| 6500 to 7000 | 14 | 8.2 | 9 | 7.1 | 8 | 9.4 | 5 | 4.7 | 82 | 4.7 |
| 7000 to 7500 | 10 | 5.9 | 5 | 3.9 | 2 | 2.4 | 2 | 1.9 | 58 | 3.3 |
| 7500 to 8000 | 3 | 1.8 | 2 | 1.6 | 1 | 1.2 | 1 | .9 | 26 | 1.5 |
| 8000 to 8500 | 3 | 1.8 | 1 | .8 | 1 | 1.2 | | | 15 | .9 |
| 8500 to 9000 | 1 | .6 | | | | | | | 3 | .2 |
| 9000 to 9500 | | | | | | | | | 2 | .1 |
| 9500 to 10000 | | | 1 | .8 | | | | | 2 | .1 |
| 10000 to 10500 | | | 1 | .8 | | | | | 3 | .2 |
| Total | 170 | 100.2 | 127 | 100.0 | 85 | 100.1 | 107 | 99.9 | 1741 | 100.0 |

type although this point cannot be accurately determined, as the histograms are quite flat-topped.

The accuracy of these conclusions is further brought out by a study of the chief physical constants of the distributions. Table 2 gives the four constants, mean, standard deviation, coefficient of variation, and skewness, together with their probable errors for each frequency of age.

TABLE 2

*Constants of variation of milk production for the successive ages at test in Jersey milk. (Eight-months lactation period.)*

| Age at test | Mean | Standard deviation | Coefficient of variation | Skewness |
|---|---|---|---|---|
| 2 yrs., 0 mos., to 3 yrs., 0 mos. | 4032.9 ± 31.7 | 818.9 ± 22.4 | 20.304 ± .577 | |
| 3 yrs., 0 mos., to 4 yrs., 0 mos. | 4686.5 ± 46.8 | 1101.5 ± 33.1 | 23.503 ± .712 | +0.2642 ± .0548 |
| 4 yrs., 0 mos., to 5 yrs., 0 mos. | 4992.9 ± 46.3 | 1079.4 ± 33.0 | 21.619 ± .684 | +0.3532 ± .0635 |
| 5 yrs., 0 mos., to 6 yrs., 0 mos. | 5281.4 ± 57.0 | 1262.8 ± 40.3 | 23.911 ± .801 | +0.3894 ± .0714 |
| 6 yrs., 0 mos., to 7 yrs., 0 mos. | 5536.5 ± 64.5 | 1325.3 ± 45.6 | 23.938 ± .865 | +0.2586 ± .0628 |
| 7 yrs., 0 mos., to 8 yrs., 0 mos. | 5314.7 ± 64.9 | 1255.0 ± 45.9 | 23.613 ± .907 | |
| 8 yrs., 0 mos., to 9 yrs., 0 mos. | 5226.4 ± 77.9 | 1302.0 ± 55.1 | 24.912 ± 1.111 | +0.3141 ± .1173 |
| 9 yrs., 0 mos., to 10 yrs., 0 mos. | 4938.2 ± 95.3 | 1302.6 ± 67.4 | 26.377 ± 1.453 | |
| 10 yrs., 0 mos., and above | 4838.8 ± 70.3 | 1077.3 ± 49.7 | 22.264 ± 1.028 | |
| Total population | 4887.6 ± 20.2 | 1249.7 ± 14.3 | 25.569 ± .310 | +0.3150 ± .0222 |

It seems best to postpone the complete discussion of the facts brought out in this table until other data to be presented are available. A few general points of especial interest may be mentioned, however. The mean milk production for the eight-months period for those cows which are between 2 and 3 years of age is 4032.9 pounds. From this point the milk production rises rapidly at first, then more slowly to a maximum at about 7 years. From this maximum the decline in milk production is less rapid toward the higher ages.

The difference between the production of 2 years and 6 months and the maximum is significant, as the difference is about 20 times its probable error (1503.6±71.9). The difference between the maximum production and that for the 10 years and above is also significant, as the difference is more than 6 times the probable error (697.7±95.40). This rise and fall of milk production with age has already been shown, by the work of this laboratory (PEARL 1914), to conform to that group of curves described by a logarithmic function.

The standard deviation varies between 818.9 pounds at the age of 2 to 3 years to 1325.3 pounds at the age of 6 to 7 years. The rise of the

standard deviation is more direct than is the rise of the mean curve. From the maximum the curve remains parallel with the base line for some years when it again drops to a lower deviation at the highest age at test. This rise and fall is significant as judged by the probable errors of the difference (PEARL 1909). The difference of the maximum standard deviation at 6 to 7 years from that at 2 to 3 years is 506.4 pounds of milk where the probable error is 50.8 pounds, or the difference is practically 10 times the probable error and the probability that this difference did not come from random sampling is considerably greater than 1,000,000,000 to 1 (ELDERTON 1901, PEARSON 1900). The difference between the maximum standard deviation and that at 10 years and above is 248.0 pounds and the probable error is 67.5 pounds or 3.68 times the probable error and the probability that this difference did not come from random sampling is 75.7 to 1. The conclusion seems justified from the above facts that the standard deviation varies with age at test in such a way that the absolute amount of the standard deviation is least at the early age, increases rapidly to a maximum at about 5 years and 6 months, remains at this maximum for about four years then falls again toward the later ages.

The coefficient of variation for the milk production of the successive ages are all high as compared with those already known for other similar data. This large size in the coefficients is brought out by table 3.

TABLE 3

*Comparison data for coefficients of variation of amount of secretion.*

| Organism | Secretion | Coefficient of variation | Source of data |
|---|---|---|---|
| Domestic fowl (Barred Plymouth Rock) | Annual egg production | 34.21 ± .37 | (PEARL 1909) |
| Cattle, British Holstein | Gallons of milk | 25.72 ± .372* | (GAVIN 1912) |
| Cattle, Ayrshire | Gallons of milk | 24.187 ± .504† | (VIGOR 1913) |
| Cattle, Jersey | Pounds of milk | 25.569 ± .310 | This paper |

* Probable error calculated by author from totals given in GAVIN's paper.

† Calculated by the author from the means and standard deviation as given by VIGOR (1913).

Of the substances studied annual egg production is the most variable. The coefficients of variation for milk production correspond remarkably well considering the diversity of the sources from which they are taken. They all go to show that milk production varies around a mean of 25, or about 9 percent less variable than egg production. This difference is significant. The mechanism of the secretion of the sum of the egg

parts to form the egg is shown to be more variable than that for the secretion of the milk parts to form the milk. Taking this reasoning back to its ultimate source, such a significant difference shows that the secretory cells of the mammary glands work with greater precision than do the cells of the oviduct. Such a difference in the precision of action of the two sets of cells would seem to indicate a greater approach to perfection, in a mechanical sense, in the cells of the udder than is true of the cells of the oviduct.

The skewness of the two sets of data furnish another interesting contrast. The skewness for annual egg production for Barred Plymouth Rock hens is —0.205 whereas the skewness for Jersey milk production is +0.315. Not only is the sign different but the actual amount is different. This cannot be explained on the basis of any selection for high producers that may have taken place, as both sets of data are about equally subject to such selection. The data for the successive age groups all go to show that where the distributions for milk production are skew they are all plus. This lends further strength to the belief that the distribution for the yearly production of the two sets of glands is skew in opposite directions. One thing is common in the two cases, the skewness in each is small in amount. This is of especial importance as it shows an approach to the value where the typical Gaussian curve of error may describe these functions.

## ANALYTICAL CONSTANTS DESCRIBING THE VARIATION OF MILK PRODUCTION AT DIFFERENT AGES

The general physical constants of milk production having been considered, the further analysis of its problems requires a knowledge of the types of frequency distributions which go to make up the lactation record of a cow during her life time. In the solution of this kind of data comes the answer to such problems as, does the type of milk-production distribution of cows milking at two years old differ from that of cows milking at three years old. This question is of great importance in considering the milking records of advanced-registry animals where it is necessary to form an opinion of the capacities of a breed from the milking abilities of a selected sample where the selection is not at random but removes those cows producing under a certain amount.

This feature of the problem is seen in the work of REITZ (1909) on the inheritance of butter-fat production in Holstein Friesian cattle.

The data for this problem came from the advanced registry of Holstein Friesian cattle. Since as a requirement to entry in this registry the cows must produce more than a certain amount of butter-fat, the correlation from such data measuring the strength of inheritance are subject to a double selection. RIETZ in correcting for this selection uses the method devised by PEARSON to determine the whole of a normal curve when a portion of it is known. The accuracy of the corrections depend then on the curves for milk production and for butter-fat percentage being normal.

The data on which this paper is based are excellent for an answer to these problems as to the types of the production curves for cows at different ages, as they represent a herd of pure-bred Jersey cows, accurately tested and recorded, constituting as near a random sample of the breed under uniform conditions as could well be found. The constants describing these distributions are given in Table 4.

TABLE 4

*Analytical constants of variation in milk production for the successive ages at test for Jersey milk. (Lactation period, eight months.)*

| Constants | 2 yrs., 0 mos., to 3 yrs., 0 mos. | 3 yrs., 0 mos., to 4 yrs., 0 mos. | 4 yrs., 0 mos., to 5 yrs., 0 mos. |
|---|---|---|---|
| Mean | 4032.89 ± 31.67 | 4686.51 ± 46.80 | 4992.91 ± 46.33 |
| Standard deviation | 818.85 ± 22.40 | 1101.47 ± 33.09 | 1079.40 ± 32.96 |
| Coefficient of variation | 20.304 ± .577 | 23.503 ± .742 | 21.619 ± .684 |
| $\mu_2$ | + 2.6821 | + 4.8529 | + 4.6604 |
| $\mu_3$ | + 0.2894 | + 5.0413 | + 6.2588 |
| $\mu_4$ | + 19.9393 | + 74.5962 | + 73.6275 |
| $\beta_1$ | 0.0043 ± .0023 | 0.2224 ± .1003 | 0.3870 ± .1391 |
| $\beta_2$ | 2.7718 ± .1362 | 3.1675 ± .3244 | 3.3900 ± .3811 |
| $\beta_2 - 3$ | − 0.2282 | + 0.1765 | + 0.3900 |
| $\kappa_1$ | − 0.4694 ± .2719 | − 0.3322 ± .4483 | − 0.3811 ± .4631 |
| $\kappa_2$ | − 0.0070 ± .0070 | − 0.5303 ± 1.2280 | −0.8361 ± 2.9443 |
| Skewness | | + 0.2642 ± .0548 | + 0.3532 ± .0635 |
| Modal divergence | | + 291.06 ± 73.48 | + 381.219 ± 75.52 |
| Mode | | 4395.45 | 4611.70 |
| Type of curve | II | I | I |
| + end of curve | 8069.15 | 17695.15 | 18896.33 |
| − end of curve | 3.36 | 1314.12 | 2351.50 |
| $y_0$ | 71.7407 | 45.9314 | 47.7073 |

TABLE 4 (continued)

*Analytical constants of variation in milk production for the successive ages at test for Jersey milk. (Lactation period, eight months.)*

| Constants | 5 yrs., 0 mos., to 6 yrs., 0 mos. | 6 yrs., 0 mos., to 7 yrs., 0 mos. | 7 yrs., 0 mos., to 8 yrs., 0 mos. |
|---|---|---|---|
| Mean | 5281.39 ± 57.04 | 5536.46 ± 64.52 | 5314.71 ± 64.92 |
| Standard deviation | 1262.84 ± 40.34 | 1325.32 ± 45.62 | 1254.98 ± 45.91 |
| Coefficient of variation | 23.911 ± .801 | 23.938 ± .865 | 23.613 ± .907 |
| $\mu_2$ | + 6.3791 | + 7.0259 | + 6.2999 |
| $\mu_3$ | + 10.1997 | + 7.5096 | + 3.0843 |
| $\mu_4$ | + 134.5412 | + 144.0314 | + 105.1169 |
| $\beta_1$ | 0.4008 ± .1436 | 0.1626 ± .0833 | 0.0380 ± .0300 |
| $\beta_2$ | 3.3063 ± .3745 | 2.9178 ± .2565 | 2.6485 ± .1655 |
| $\beta_2 - 3$ | + 0.3063 | — 0.0822 | — 0.3515 |
| $\kappa_1$ | — 0.5898 ± .4413 | — 0.6523 ± .3714 | — 0.8171 ± .3021 |
| $\kappa_2$ | — 0.5619 ± .5240 | — 0.1952 ± .1928 | — 0.0354 ± .0347 |
| Skewness | + 0.3894 ± .0714 | + 0.2586 ± .0628 | |
| Modal divergence | + 491.70 ± 103.81 | + 342.77 ± 107.10 | |
| Mode | 4789.69 | 5193.69 | |
| Type of curve | I | I | II |
| + end of curve | 16682.37 | 13960.06 | 10186.64 |
| — end of curve | 2430.70 | 1961.51 | 442.78 |
| $y_0$ | 35.9420 | 28.3749 | 25.6501 |

TABLE 4 (continued)

*Analytical constants of variation in milk production for the successive ages at test for Jersey milk. (Lactation period, eight months.)*

| Constants | 8 yrs., 0 mos., to 9 yrs., 0 mos. | 9 yrs., 0 mos., to 10 yrs., 0 mos. | 10 yrs., 0 mos., and above |
|---|---|---|---|
| Mean | 5226.38 ± 77.92 | 4938.24 ± 95.30 | 4838.79 ± 70.25 |
| Standard deviation | 1301.98 ± 55.10 | 1302.56 ± 67.38 | 1077.28 ± 49.67 |
| Coefficient of variation | 24.912 ±1.111 | 26.377 ± 1.453 | 22.264 ± 1.028 |
| $\mu_2$ | + 6.7806 | + 6.7867 | + 4.6421 |
| $\mu_3$ | + 13.8706 | + 1.1758 | + 1.4117 |
| $\mu_4$ | + 201.7722 | + 118.7966 | + 60.7500 |
| $\beta_1$ | 0.6171 ±.4429 | 0.0044 ± .0497 | 0.0199 ± .0150 |
| $\beta_2$ | 4.3886 ± 1.7775 | 2.5792 ± .2166 | 2.8191 ± .2517 |
| $\beta_2 - 3$ | + 1.3883 | — 0.4208 | — 0.1809 |
| $\kappa_1$ | + 0.9258 ± 2.4700 | — 0.8548 ± .3509 | — 0.4216 ± .4975 |
| $\kappa_2$ | + 0.5794 ± 1.4184 | — 0.0039 ± .0051 | — 0.0357 ± .0424 |
| Skewness | + 0.3141 ± .1173 | | |
| Modal divergence | + 408.93 ± 156.62 | | |
| Mode | 4817.45 | | |
| Type of curve | IV | II | II |
| + end of curve | + ∞ | 9498.86 | 10852.89 |
| — end of curve | — ∞ | 377.61 | 1175.32 |
| $y_0$ | .0014 | 12.2016 | 19.3754 |

TABLE 4 (continued)

*Analytical constants of variation in milk production for the successive ages at test for Jersey milk. (Lactation period, eight months.)*

| Constants | Total population |
|---|---|
| Mean | 4887.56 ± 20.21 |
| Standard deviation | 1249.71 ± 14.28 |
| Coefficient of variation | 25.569 ± .310 |
| $\mu_2$ | + 6.2471 |
| $\mu_3$ | + 9.6623 |
| $\mu_4$ | + 138. 3606 |
| $\beta_1$ | 0.3829 ± .0613 |
| $\beta_2$ | 3.5454 ± .1979 |
| $\beta_2 - 3$ | + 0.5454 |
| $\kappa_1$ | − 0.0581 ± .2582 |
| $\kappa_2$ | − 5.4182 ± * |
| Skewness | + 0.3150 ± .0222 |
| Modal divergence | + 393.65 ± 29.91 |
| Mode | 4493.91 |
| Type of curve | I |
| + end of curve | 95879.24 |
| − end of curve | 1029.4 |
| $y_0$ | 288.674 |

* Probable error very large.

Attention may be directed first to the moments of the individual distributions of milk production for the groups of the successive yearly ages. The third moment is consistently plus and on the whole rather small. The moments lead to values of $\beta_1$ which are rather small. In no case is the value so great as three times its probable error. $\beta_2$ is likewise only slightly different from the value 3 demanded by the normal curve. In no case is this difference as great as three times its probable error. Out of the nine age groups into which the data have been divided $\beta_2$—3 is plus four times and minus five times. No consistency is shown in the sign and it seems safe to say its change of direction comes from random sampling. The sign of $\kappa_1$ is plus once and minus eight times; its value in no case exceeds three times its probable error. The sign of $\kappa_2$ is of course, governed by that of $\kappa_1$. The absolute value varies between 0.0039 and 0.8361. The values of the probable errors are all large in comparison with the values of $\kappa_2$.

These facts all lead to the conclusion that no great confidence can be placed in either the sign or the absolute magnitude of the criterion for the frequency type. Such big probable errors of $\kappa_1$ and $\kappa_2$ suggest that all of the curves are near the critical limit of more than one type of frequency curve. The problem now becomes: what is the chance that

a frequency distribution, other than that indicated by the criteria may be obtained to fit the data equally well. It is necessary therefore to turn to the probable errors of the frequency type itself to determine this question. The tables and diagrams necessary for the speedy determination of this have been calculated by RHIND (1909). Comparison of the values of $\Sigma_1$ $\Sigma_2$ with diagram for the frequency type contained in this paper together with the other necessary calculations shows the types indicated in table 4 should give a good fit.

The distributions for the successive ages are shown to be equally types I and II with one which is type IV. Five of the curves are skew and four symmetrical; eight are limited in range in both directions and one is unlimited in range. The equations to these curves are as follows.

Age at test 2 years to 3 years:

$$y = 71.7407\left(1 - \frac{x^2}{16{,}291{,}354}\right)^{10.648}$$

Age at test 3 years to 4 years:

$$y = 45.9314\left(1 + \frac{x}{3081.32}\right)^{6.2322}\left(1 - \frac{x}{13299.70}\right)^{26.8997}$$

Age at test 4 years to 5 years:

$$y = 47.7073\left(1 + \frac{x}{2260.20}\right)^{4.0347}\left(1 - \frac{x}{14284.63}\right)^{25.4999}$$

Age at test 5 years to 6 years:

$$y = 35.9420\left(1 + \frac{x}{2358.99}\right)^{2.8776}\left(1 - \frac{x}{11892.68}\right)^{14.5074}$$

Age at test 6 years to 7 years:

$$y = 28.3749\left(1 + \frac{x}{3232.17}\right)^{3.8103}\left(1 - \frac{x}{8766.38}\right)^{10.3344}$$

Age at test 7 years to 8 years:

$$y = 25.6501\left(1 - \frac{x^2}{23{,}735{,}702}\right)^{6.0352}$$

Age at test 8 years to 9 years:

$$y = .0014\left(1 + \frac{x^2}{12{,}094{,}088}\right)^{-9.9809} e^{21.0802 \tan -1 \frac{x}{3477.66}}$$

Age at test 9 years to 10 years:

$$y = 12.2016\left(1 - \frac{x^2}{20{,}799{,}307}\right)^{4.6294}$$

Age at test 10 years and above:

$$y = 19.3754\left(1 - \frac{x^2}{36{,}169{,}519}\right)^{14.0831}$$

Total population:

$$y = 288.674\left(1 + \frac{x}{3464.52}\right)^{8.086}\left(1 - \frac{x}{91385.33}\right)^{213.294}$$

The histograms and the fitted curves for the milk production of the individual ages are shown in figure 1. All of the areas have been reduced to a percentage base so that the ordinates and areas of each distribution could be compared directly.

It is clear to the eye that on the whole the graduation of the data by the fitted curves is rather good. Measured mathematically by the test of goodness of fit (ELDERTON 1901; PEARSON 1900) of the theoretical curve to the raw data the value of P ranges between 0.5864 and 0.9942 as shown by table 5.

TABLE 5

*Values of P for the fit of the theoretical curves to the observational curves for milk production of Jersey cattle.*

| Age at test | P |
|---|---|
| 2 years to 3 years | 0.6680 |
| 3 years to 4 years | 0.8453 |
| 4 years to 5 years | 0.9114 |
| 5 years to 6 years | 0.9424 |
| 6 years to 7 years | 0.9942 |
| 7 years to 8 years | 0.9145 |
| 8 years to 9 years | 0.5864 |
| 9 years to 10 years | 0.6873 |
| 10 years and above | 0.9602 |

This table brings out the excellence of the graduation of the data by the frequency curves.

As previously stated eight of the nine curves are of limited range in both directions and one of unlimited range in either direction. The limits of these ranges are of especial interest since they indicate the highest and lowest milk production expected for a given age. It is evi-

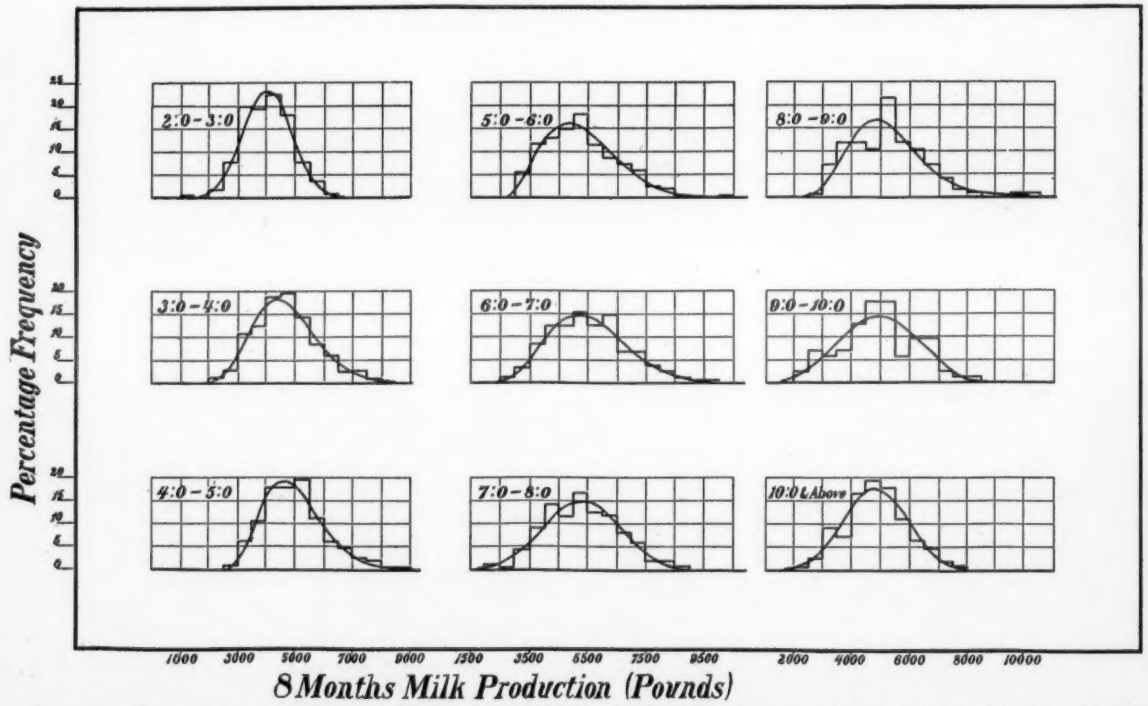


FIGURE 1.—Histograms and fitted curves showing the variation of milk production for each year of age. The area of each curve is reduced to unity so that any distribution of a given age may be compared with ony other at another age. The relative increase in the height of the model ordinates at the lower and higher ages of lactation as compared with the ages 6 to 10 years is quite evident. The fitted curves are all PEARSON type curves the constants of which are seen in table 4.

dent that in the symmetrical curves (type II) the plus end of the range is not as high as in the type I curves, in fact, the end of the range of high milk producers is rather underestimated than overestimated. The type I curves estimate the highest expected milk production at what we might consider a fair estimate. Thus, Jersey cows 3 years to 4 years old would not be expected to produce more than 17,695 pounds of milk in 8 months. This is borne out by the actual experience of the breed. The figure 10,186 for the 8-months production in the 7-year to 8-year class is low, however, compared with the production of certain REGISTRY-OF-MERIT cows; e.g., Passport is known to have produced 19,694 pounds in one year. Such a difference in the plus end of the range would seem to indicate a real difference of this group of Jerseys from those of the advanced registry group in the direction of an extended range for the REGISTRY-OF-MERIT animals.

The minus end of the range is equally interesting. The type II curves again do not give as good an estimate as the type I. They are in most cases too low. The low end of the production scale for this group of cattle is on the whole pretty well estimated, however. For the data themselves we have one observation as low as 1250-pound group. The estimate for this particular range is on the whole rather low (3.36 pounds of milk). In any case the author has in his note-book a record of milk production for one year of an Aberdeen Angus cow at 6 years 6 months of only 244.7 pounds which is not so far different from the above low-range estimate. Such records as these show us that the low margin of production is not on the whole overestimated. In all of this work it must also be remembered that the limited- and unlimited-range curves have only a small frequency at these points. Thus the fact that we have one curve whose range is not limited should not trouble us, as the frequencies of this range beyond the customary limits, become very small indeed.

All of the curves are of the mesokurtic type as the values of $\beta_2$—3 are small and in each case less than three times the probable error of $\beta_2$. Furthermore the sign of the kurtosis is plus in four cases and minus in five showing more clearly if necessary the mesokurtic nature of all of the distributions.

The changes in the position of the modal ordinate with increasing age generates a curve rising almost linearly to its high point at a production of 5314 pounds for 7 years and 6 months. From this high point it falls toward a lower production for the maximum frequency of the older cows.

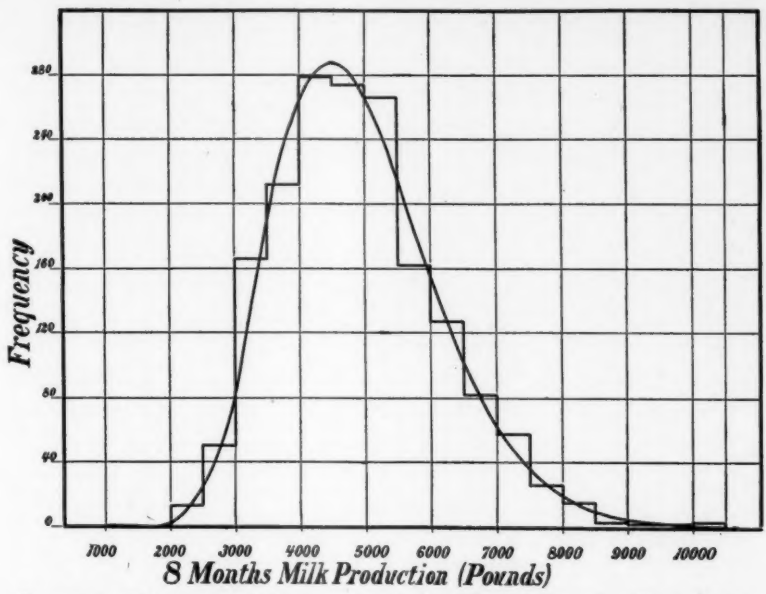


FIGURE 2.—Histogram and fitted curve showing the variation of milk production that may be expected to occur in a pure-bred Jersey herd without regard to age. It is evident that by and large the curve strikes through the observation well. The distribution of milk production is seen in general to be quite skew.

The variation of the total population of Jersey milk production is valuable both for itself and for comparison with other breeds. Table 4 gives the necessary constants for the calculation of the frequency curve suitable to fit the data. Figure 2 shows these data graphically.

The theoretical curve for these data is type I as the values of $\beta_1$ and $\beta_2$ are such as to lead to a $\kappa_2$ of —5.4182 calling for a type I curve. The curve is significantly skew in the plus direction. The range of this curve much more than covers the actual observations and goes a good deal beyond the probable value of the milk production of any cow in describing the highest milk production expected. This is no doubt due to the fact that toward the plus end of the range the observed frequency of high-producing cows trails off slowly. The minus end of the range is well described.

As shown by the above data the assumption previously indicated in the study of milk inheritance by RIETZ is open to the criticism that the distributions of milk production at a given age are not normal curves

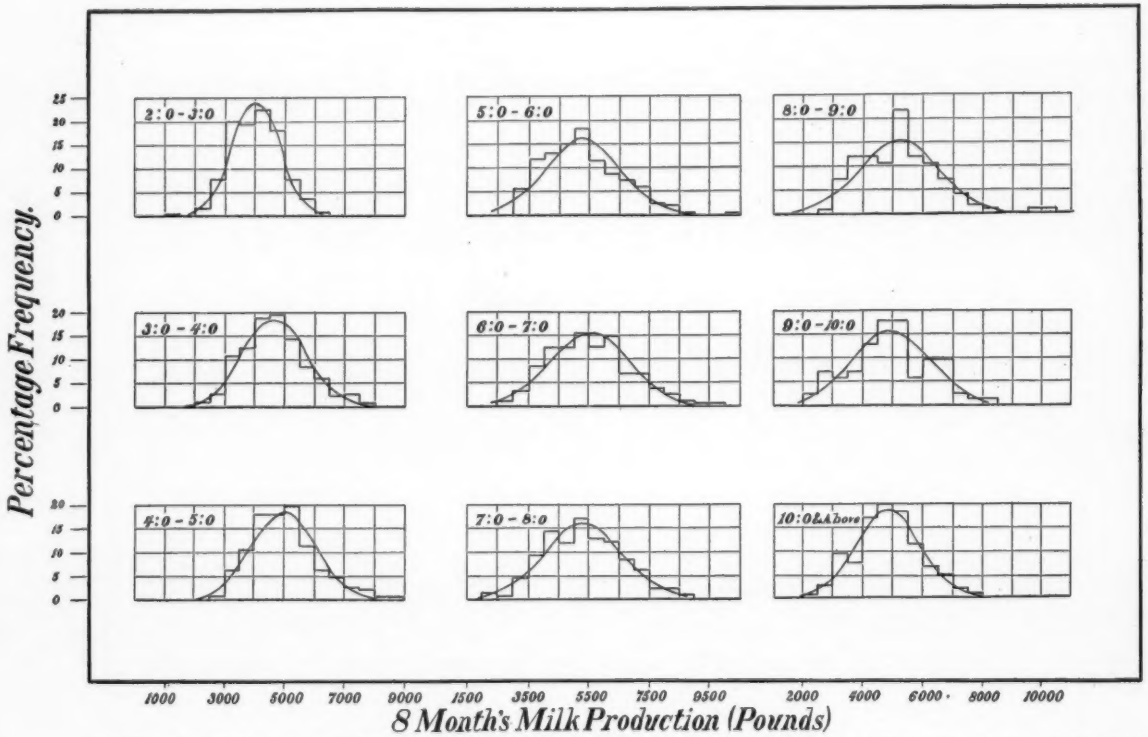


FIGURE 3.—Histograms and fitted curves showing the variation of milk production of each year of age. The fitted curves in this case are all normal curves calculated from table 4. The histograms are the same as those of figure 1. Each distribution is drawn on a basis of area equal to one, so that each curve is directly comparable with others. It is evident that the fit as a whole is not as good as in figure 1, especially at the ends of the range.

but belong in general to the type I and type II curves. The problem becomes that of how great an error is introduced by regarding the data as described by normal curves. Normal curves have been fitted to the above data to make the comparison. These curves together with their corresponding histograms are shown in figure 3.

In comparison with figure 1 the normal curves are seen in general to describe the tail frequencies poorly. The P for the fit of these curves are shown in table 6.

TABLE 6

*Values of P for the fit of the theoretical normal curves to the observational curves for milk production of Jersey cattle.*

| Age at test | P |
|---|---|
| 2 years to 3 years | 0.4335 |
| 3 years to 4 years | 0.4130 |
| 4 years to 5 years | 0.0943 |
| 5 years to 6 years | 0.7442 |
| 6 years to 7 years | 0.7450 |
| 7 years to 8 years | 0.8532 |
| 8 years to 9 years | 0.5517 |
| 9 years to 10 years | 0.5083 |
| 10 years and above | 0.9333 |

These data (table 6) show that normal curves do not describe milk production at different ages as well as do the proper type curve. The difference in the fit of the type curves over the normal curve comes especially in the description of the tails and the skewness of these distributions. The fit of the normal curves is not bad, however, and in all probability no serious error would be made in the use of them for the determination of the corrections to be applied to the correlations from double-selected data as was done by RIETZ.

## THE CORRELATION OF JERSEY 8-MONTHS MILK PRODUCTION WITH THE AGE AT TEST

Common knowledge among dairymen is that milk production and age at the commencement of the lactation are correlated in such a way that advancing age means increased production. The opinion is general that this increase is a linear one. This opinion has been shown to be erroneous by previous work of this laboratory (PEARL 1914) on the statistics of the 7-day records of American Jersey cattle found in "Jersey sires with their tested daughters," published by the AMERICAN JERSEY

CATTLE CLUB. In this work seven-day milk production is shown to be a logarithmic curve and not a straight line.

It remains to be shown what is the curve describing a true random sample of the Jersey breed for a longer milking period. Data of this sort is important for several reasons, chief among which, both practically and theoretically, is the necessity of having suitable correction factors for age to allow comparison of milk records at different periods in the lives of different cows. Toward the solution of this problem the following facts are necessary: What correlation exists between age and milk production? Is this correlation sufficient so that it must be taken into account in considering records of different cows at different ages? What is the equation of the regression line between these two variables? Table 7 furnishes the data necessary for this study.

The correlation and its accompanying constants for these two variables are shown in table 8.

TABLE 8

*Constants measuring the association between amount of eight-months milk produced and age at test of Jersey cows.*

| $r$ | $\eta$ | $\eta - r$ | $\eta^2 - r^2$ |
|---|---|---|---|
| 0.2596 ± .0151 | 0.4283 ± .0132 | 0.1689 ± .0201 | 0.1161 ± .0108 |

This table makes clear several facts concerning the influence of age on milk production. The correlation of $+0.2596 \pm .0151$ shows that age at test and milk production are significantly correlated variables. Taken in conjunction with the correlation ratio it shows clearly that age of the cow at commencement of test must be considered in comparing the records of different cows if the conclusion from the comparison is to be valid. The value of the correlation ratio $+0.4283 \pm .0132$ is considerably higher than the correlation coefficient. This difference is shown to be highly significant by the value of $\eta - r = 0.1689 \pm .0201$. It is altogether probable therefore that the regression of age on milk production is a skew regression. This is shown to be a fact by the constant to measure such skewness. $\eta^2 - r^2$, $0.1161 \pm .0108$, is about 11 times its probable error. The regression is therefore known to be skew. Since this is true the correlation ratio is a better measure of the true correlation than is the correlation coefficient. The relation of age at test is then doubly significant in any comparison of the records of two cows. The regression having been shown to be skew it becomes necessary to deal with it separately.

TABLE 7.

*Correlation surface for pounds of milk and age at test for Jersey cattle. (Lactation period, eight months.)*

| | 1000-1500 | 1500-2000 | 2000-2500 | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | 9000-9500 | 9500-10000 | 10000-10500 | 10500-11000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1:6- 2:0 | | | | 5 | 15 | 10 | 2 | 2 | | | | | | | | | | | | | 34 |
| 2:0- 2:6 | 1 | | 4 | 19 | 54 | 51 | 56 | 42 | 19 | 7 | 2 | | | | | | | | | | 255 |
| 2:6- 3:0 | | | 1 | 4 | 6 | 7 | 11 | 12 | 4 | 4 | | | | | | | | | | | 49 |
| 3:0- 3:6 | | | | 4 | 21 | 22 | 33 | 30 | 20 | 13 | 8 | 3 | 2 | | | | | | | | 156 |
| 3:6- 4:0 | | | 3 | 3 | 6 | 9 | 14 | 19 | 16 | 8 | 7 | 3 | 5 | 2 | 1 | | | | | | 96 |
| 4:0- 4:6 | | | | 2 | 8 | 15 | 31 | 24 | 25 | 15 | 7 | 8 | 1 | 2 | | 1 | | | | | 139 |
| 4:6- 5:0 | | | | | 7 | 11 | 13 | 20 | 24 | 13 | 8 | 3 | 5 | 3 | 1 | | | | | | 108 |
| 5:0- 5:6 | | | | | 7 | 13 | 16 | 14 | 23 | 10 | 5 | 7 | 9 | 2 | 1 | 1 | | | | | 108 |
| 5:6- 6:0 | | | | | 5 | 13 | 12 | 19 | 17 | 15 | 14 | 9 | 4 | 3 | 3 | | | | 1 | | 115 |
| 6:0- 6:6 | | | | 2 | 2 | 10 | 14 | 8 | 14 | 12 | 12 | 5 | 6 | 3 | 3 | | | 1 | | | 92 |
| 6:6- 7:0 | | | | | 4 | 6 | 9 | 15 | 15 | 12 | 16 | 8 | 7 | 4 | 1 | | 2 | | 1 | | 100 |
| 7:0- 7:6 | | | 2 | 1 | 4 | 5 | 16 | 11 | 19 | 7 | 6 | 5 | 5 | 2 | | | | | | | 82 |
| 7:6- 8:0 | | | | | 3 | 11 | 8 | 9 | 9 | 14 | 14 | 9 | 5 | 1 | 3 | 1 | | | | | 87 |
| 8:0- 8:6 | | | | 1 | 7 | 7 | 7 | 10 | 15 | 8 | 7 | 4 | 2 | 1 | 1 | | | | 1 | | 71 |
| 8:6- 9:0 | | | | | 2 | 8 | 8 | 3 | 12 | 7 | 6 | 5 | 3 | 1 | | | | 1 | | | 56 |
| 9:0- 9:6 | | | 1 | 3 | 4 | 3 | 7 | 9 | 7 | | 3 | 5 | 1 | | | | | | | | 43 |
| 9:6-10:0 | | | 1 | 3 | 1 | 3 | 4 | 6 | 8 | 5 | 5 | 3 | 1 | 1 | 1 | | | | | | 42 |
| 10:0-10:6 | | | | | 1 | 1 | 3 | 9 | 6 | 1 | 1 | 4 | | | | | | | | | 26 |
| 10:6-11:0 | | | 1 | | 3 | 3 | 2 | 2 | 4 | 3 | 3 | 1 | 1 | 1 | | | | | | | 24 |
| 11:0-11:6 | | | | 1 | 3 | 2 | 6 | 5 | 3 | 4 | 1 | | 1 | | | | | | | | 26 |
| 11:6-12:0 | | | | | | | 2 | 1 | 1 | | 1 | | | | | | | | | | 5 |
| 12:0-12:6 | | | | 1 | 3 | | | 2 | 1 | 2 | | | | | | | | | | | 9 |
| 12:6-13:0 | | | | | | 1 | 2 | 1 | 2 | 1 | | | | | | | | | | | 7 |
| 13:0-13:6 | | | | 1 | | 1 | 1 | | 1 | 1 | | | | | | | | | | | 5 |
| 13:6-14:0 | | | | | | | 1 | | | | 1 | | | | | | | | | | 2 |
| 14:0-14:6 | | | | | | | | 1 | 1 | | | | | | | | | | | | 2 |
| 14:6-15:0 | | | | | | | | | | | | | | | | | | | | | 0 |
| 15:0-15:6 | | | | | | | 1 | | | | | | | | | | | | | | 1 |
| 15:6-16:6 | | | | | | | | | | | | | | | | | | | | | |
| Total | 1 | 0 | 13 | 50 | 166 | 212 | 279 | 274 | 266 | 162 | 127 | 82 | 58 | 26 | 15 | 3 | 2 | 2 | 3 | | 1741 |

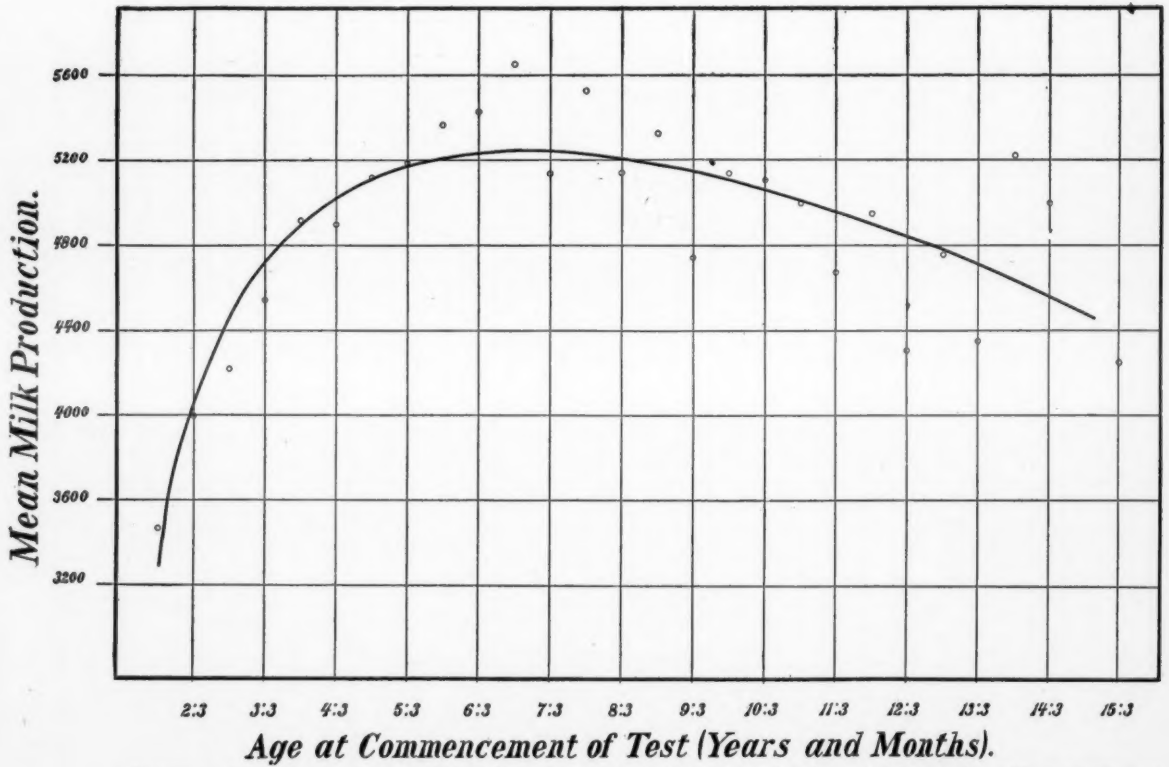


FIGURE 4.—Diagram showing the observed means and theoretical means for Jersey eight-months milk production at any given age. The observed means are calculated from table 7. The curve as a whole is evidently of the logarithmic type described well by the theoretical curve the constants of which are given below. The observations are represented as the small circles.

## TYPES OF THE REGRESSION OF MILK PRODUCTION ON AGE OF JERSEY CATTLE

The means for each array of age of table 6 have been calculated. These means are indicated by points within circles in figure 4.

Examination of the observational curve in figure 4 shows that it takes the general form of a logarithmic curve, agreeing in this respect with the other data from this laboratory (PEARL 1914). From these means the theoretical curve conforming to the general logarithmic type has been calculated by the method of least squares. The equation to this curve is

$$y = 3387.912 - 99.883x - .487x^2 + 2896.219 \log x$$

where $x$ is taken in six-months intervals from an origin at 1 year and 3 months.

The observations at the higher ages vary a good deal as they are based on small numbers. The theoretical curve strikes through them quite accurately when the unevenness of the observed curve is considered. When we calculate the $\chi^2$ by the method of SLUTSKY (1914) we find that 5 observations contribute a sum of 28.80 to the total of 45.41. These observations are at ages 2 years 9 months, 3 years 3 months, 6 years 9 months, 7 years 9 months and 9 years 3 months. If we measure the fit by the total $\chi^2$, 45.41, it is poor. Considering the above-mentioned five observations in connection with the other observations it is seen that two of them are plus and three are minus quantities. Not only that but they come at places in the curve so that they could practically counteract each other if the first smoothed curve were used as the observational. It seems altogether reasonable therefore to consider the fit of this curve measured by a $\chi^2$ somewhat more than 17.00 or what would correspond to the P of a very good fit.

The equation of the curve has many practical uses aside from its interest in a scientific sense. By its use the records of cows at different ages may be brought to the same basis for comparison whether it be for milk-inheritance studies, analysis of judging experiments or the like. The time of the theoretical maximum of milk production may be easily calculated from it by differentiation. This maximum is shown to be 7 years 2.4 months, a figure considerably above the age customarily called mature form. Further the curve shows that the method used in advanced-registry work of determining the amount a Jersey cow should produce for the REGISTER OF MERIT is fallacious in that it is a linear method and does not recognize this logarithmic nature of milk production. In a previous paper (GOWEN 1919) the average fat percent of

Jersey cows is given as 5.12. Assuming this figure and dividing the pounds of butter-fat by it gives us the average requirement for milk production in one year. Supposing that ¾ of the year's records is made in the first 8 months of lactation (a figure reasonably close to the expected (PEARL 1915)) the required production is found to be 3600 pounds at 2 years and 5200 pounds at 5 years. From figure 3 it is evident therefore that if a cow is to be pushed for the advanced registry the best time to get her in, is to have her calve at about 3 years 3 months of age.

Causally considered the logarithmic nature of milk production is of a good deal of interest. The work of a number of students of growth, beginning with MINOT's (1891) notable studies on rabbits and guinea-pigs has shown that the phenomena of growth are also a logarithmic function of age. This law appears of wide general application as the work of LEWENZ and PEARSON (1904) have shown that it holds for growth in children; DONALDSON (1908, 1909, 1910, 1911), HATAI (1911) and JACKSON (1913) have shown it to be of general application to the growth of certain organs in the white rat; PEARL (1907) and PEARL and SURFACE (1915) have shown it to be true for Ceratophyllum and maize. It seems, therefore, altogether likely that the mammary glands of the cow also follow this rule. Should this prove true the increase of milk production with age seems of much significance in paralleling these growth phenomena. This paralleling of the two functions would in fact seem to indicate a causal relation between the two in that the increase in milk production may depend chiefly on the increase in actual mass of the mammary gland due to growth of this organ and not due to any relative increase in the ability of the cells to secrete more milk.

## THE NATURE OF THE CURVE OF THE STANDARD DEVIATION OF MILK PRODUCTION

The curve found by plotting the standard deviations of 8-months milk production for each six months age intervals is shown in figure 4. The circles represent the actual standard deviations of the age arrays calculated from table 7. A glance at these suffices to show that the curve is not the customary linear one. It has rather the appearance of a parabola or logarithmic curve. The actual choice of the type of curve describing these data, other things being equal, depends on the fit of the theoretical curve to the observational data. Accordingly two curves

were tried, a cubic parabola having the form $y = a + b\,x + c\,x^2 + d\,x^3$, and a logarithmic curve $y = a + bx + cx^2 + d \log x$. These two curves were chosen as they had the same number of constants. The cubic fitted to the data by the method of MINER (1917) gave the equation to the data as

$$y = 399.46 + 188.82\,x - 11.664\,x^2 + 0.1919\,x^3.$$

The logarithmic curve was

$$y = 497.08 + 4.025\,x - 1.689\,x^2 + 909.13 \log x$$

The fit of these curves to the observational data was then compared by calculating for each the mean error and the root mean-square error. These values will of course be very large from the evident unevenness of the observation curve, they will however serve as a good comparative measure. The mean error for the parabola is 99.6, the root mean square error 132.0; for the logarithmic curve the mean error is 102.3 and the root mean square error 133.5. From this comparison the cubic parabola fits the data most accurately. Figure 5 shows the observation and

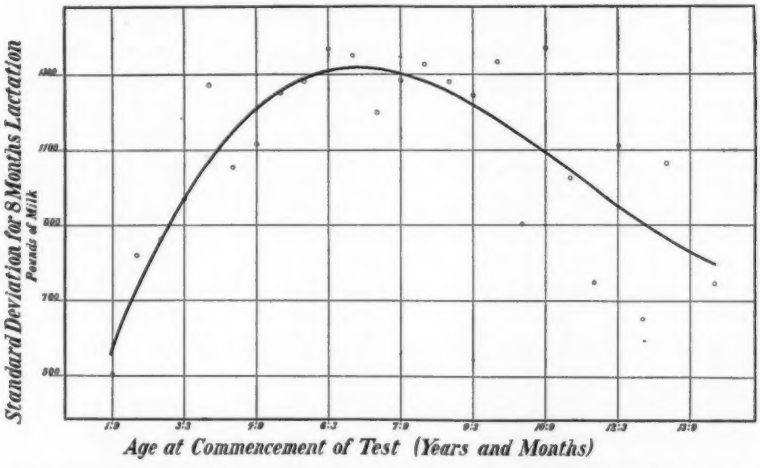


FIGURE 5.—Observational and theoretical curve for the standard deviations of milk production for the successive ages at which the lactation commenced. The theoretical curve is the cubic parabola given above. Considering the large variation of the observed standard deviations the cubic strikes through the observations well.

fitted cubic. The cubic parabola is seen by the figure to strike through the observation very well.

If we define with PEARSON (1905) the scedastic curve as the curve

formed by the ratios of standard deviations of the $x$ arrays of $\beta$ divided by the standard deviation of $\beta$ plotted to $x$, then it is evident that the standard-deviation lines of milk production show that the value of $\eta$ is will form, when divided by the standard deviation of milk production at all ages, a curve similar in shape to the curve plotted in figure 5. Milk production with age is therefore heteroscedastic. As the change in the scedastic curve follows a regular system the curve is nomic.

The facts brought forth in the discussion of the regression and standard-deviation lines of milk production show that the value of $\eta$ is nearer the value of the true correlation of milk production with age than is the value of $r$. It therefore strengthens more strongly if need be the argument of age correction in all milk-production studies involving comparisons of milk production at different times in a cow's life.

## THE CORRELATION BETWEEN THE MILK YIELD OF ONE LACTATION AND THAT OF SUCCEEDING LACTATIONS

### *Mean milk production of cows retained long or short periods in the herd*

Up to this point the discussion has dealt entirely with the influence of age on amount of milk produced in a given lactation and the variability of the milk produced during it. In the present section the phase of the problem dealing with one lactation in its relation to another will be considered.

The functioning of the mammary glands may be considered dependent upon three main factors, which, taken in order of their natural sequence are: heredity; development through feeding, etc. (environmental circumstances), of these organs up to their commencing to secrete; and lastly environmental factors in their widest sense acting during the months when the gland is active. It is reasonably clear that on our ability to distinguish the relative influence of these three basic variables depends many of the common *a priori* dairy practices as well as furnishing a solid foundation for the analysis of the causal mechanism of milk production itself. The analysis is a complex one and needs to be attacked by many channels. The present investigation was undertaken in the hope that by an analysis of the intra-individual variation of milk secretion from lactation to lactation some light would be given on the relative merits of these three variables. The homogeneous nature of the material is such, however, that the investigation necessarily deals chiefly with the first of these variables.

Little work on milk secretion has been done that approaches the problem from this viewpoint. Of the available data those on the English herds analyzed by GAVIN (1913) are undoubtedly the best. This investigation on a mixed herd of British Holsteins and grade Short Horns furnishes data of value for the records of the first lactation in comparison with the yields of subsequent lactations. In all of this work the measure of the lactation used is what he designates as the "revised maximum," this term being defined as the maximum day yield of the lactation which is three times reached or exceeded. These results are considered largely for their strictly practical bearing. They are of little use to the American farmer in that he is accustomed to deal with records over a certain limit of time and not maximum productions. These facts make it evident that no repetition in either data or aim of the investigation occurs in these studies. The constants derived by GAVIN will be of a good deal of interest for comparison with those presented here as together they show the range of variation to be expected under the different conditions of England and the United States, a mixed herd and a pure-bred herd, and a difference in the measure of the lactating capacity from lactation to lactation.

The preliminary steps should include a study of the population of each frequency which is to be compared. The data for this comparison are taken from the correlation tables beginning with number 9 and ending with 40.

TABLE 9

*Correlation surface for amount of eight-months milk production at two years old and amount of eight-months milk production at three years old for pure-bred Jersey cows.*

| 2 years old \ 3 years old | 2000-2500 | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | | | 1 | | | | | | | | | | | 1 |
| 2500-3000 | | | 1 | 5 | 5 | | | | | | | | | 11 |
| 3000-3500 | 1 | 1 | 8 | 5 | 11 | 5 | 1 | 1 | | | | | | 33 |
| 3500-4000 | | | 3 | 6 | 11 | 11 | 5 | 3 | | | | | | 39 |
| 4000-4500 | | | 2 | 2 | 4 | 11 | 7 | 4 | 3 | 1 | 1 | | | 35 |
| 4500-5000 | | 2 | 2 | 2 | 4 | 8 | 6 | 6 | 7 | 2 | | | | 39 |
| 5000-5500 | | | | | | 2 | 5 | 2 | 2 | 1 | 3 | 1 | 1 | 17 |
| 5500-6000 | | | 1 | | 1 | 2 | | | 1 | 1 | 1 | | | 7 |
| 6000-6500 | | | | | | | | | | | 1 | 1 | | 2 |
| Total | 1 | 3 | 18 | 20 | 36 | 39 | 24 | 16 | 13 | 5 | 6 | 2 | 1 | 184 |

TABLE 10

*Correlation surface for amount of eight-months milk production at two years old and amount of eight-months milk production at four years old for pure-bred Jersey cows.*

| 2 years old \ 4 years old | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2500-3000 | 1 | 4 | 4 | | 2 | | | | | | | | 11 |
| 3000-3500 | 5 | 6 | 10 | 2 | 5 | 1 | | | | | | | 29 |
| 3500-4000 | 12 | 3 | 7 | 7 | 8 | 3 | | 1 | | | | | 41 |
| 4000-4500 | 2 | 2 | 5 | 6 | 9 | 4 | 7 | 3 | 1 | 1 | 1 | | 41 |
| 4500-5000 | 1 | | 5 | 6 | 8 | 7 | 1 | 2 | 3 | | | | 33 |
| 5000-5500 | | | 1 | 2 | 2 | 1 | 1 | 3 | 2 | 1 | | | 13 |
| 5500-6000 | | | | | 1 | 1 | 2 | 1 | | | | 1 | 6 |
| Total | 21 | 15 | 32 | 23 | 35 | 17 | 11 | 10 | 6 | 2 | 1 | 1 | 174 |

The tabled constants are presented in the following order, (1) the means of each of the compared populations (table 11), (2) the standard deviations of each of the compared populations (table 20), and the coefficients of variation of each of the compared populations (table 25). The vertical columns of each table present the means, standard deviations, etc., of the age indicated when correlated with each of the lactation records made at the age on the left of the table. Thus, the means of the 8-months' milk production of the two-year group that is correlated with the three-year group, is 4141.30 pounds of milk. The value of the mean production in this column should of course be the same if the population of milk production of the two-year group is the same for the cows kept to their three-year-old lactation as it is for the cows kept to their seven-year-old lactation. Table 11 presents the data for the comparisons of these mean milk productions.

TABLE 11

*Mean 8-months milk production of a given age when correlated with other given ages.*

| Age | 2-3 | 3-4 | 4-5 | 5-6 |
|---|---|---|---|---|
| 2 to 3 | | 4796.20 ± 55.15 | 4962.64 ± 59.63 | 5542.86 ± 74.47 |
| 3 to 4 | 4141.30 ± 40.12 | | 5031.05 ± 60.19 | 5344.41 ± 80.52 |
| 4 to 5 | 4091.95 ± 37.66 | 4642.16 ± 57.56 | | 5190.55 ± 67.40 |
| 5 to 6 | 4178.57 ± 44.62 | 4739.51 ± 04.10 | 5033.22 ± 59.05 | |
| 6 to 7 | 4192.62 ± 48.71 | 4819.57 ± 72.78 | 5141.67 ± 67.93 | 5401.64 ± 76.40 |
| 7 to 8 | 4156.59 ± 58.81 | 4867.35 ± 77.53 | 5143.81 ± 65.17 | 5315.89 ± 65.87 |
| 8 to 10 | 4061.93 ± 48.09 | 4698.11 ± 75.14 | 5067.07 ± 62.08 | 5298.28 ± 69.64 |
| 10 and older | 4162.50 ± 66.27 | 5171.05 ± 199.66 | 4994.90 ± 103.53 | 5468.18 ± 65.79 |

TABLE 11 (continued)

*Mean 8-months milk production of a given age when correlated with other given ages.*

| Age | 6-7 | 7-8 | 8-10 | 10 and older |
|---|---|---|---|---|
| 2 to 3 | 5754.10 ± 88.77 | 5464.29 ± 86.47 | 5094.04 ± 81.11 | 4925.00 ± 119.59 |
| 3 to 4 | 5710.87 ± 89.16 | 5459.18 ± 87.31 | 5099.06 ± 91.12 | 4907.89 ± 144.32 |
| 4 to 5 | 5612.50 ± 104.63 | 5435.84 ± 80.10 | 5152.44 ± 78.20 | 4760.20 ± 101.39 |
| 5 to 6 | 5631.15 ± 83.22 | 5521.32 ± 73.79 | 5208.62 ± 75.90 | 4868.18 ± 108.99 |
| 6 to 7 | | 5334.68 ± 78.04 | 5189.19 ± 71.69 | 4914.06 ± 84.65 |
| 7 to 8 | 5399.19 ± 115.94 | | 5081.13 ± 74.40 | 4831.08 ± 85.76 |
| 8 to 10 | 5371.62 ± 74.90 | 5220.20 ± 63.66 | | 4903.23 ± 69.14 |
| 10 and older | 5382.81 ± 61.45 | 5195.94 ± 83.20 | 5185.48 ± 69.65 | |

The data presented in this table are graphically represented in figure 6. In this figure the mean 8-months milk production is given at the left. The line at the top of the figure represents the mean milk production of the two-year-olds that had lactations at the other ages shown on the lower margin of the figure. The next line down represents the 3-year mean production when compared with the other ages, etc. The ages with which these are compared are shown in the bottom margin of the figure. The lines generated by the mean productions of each of these age groups should, of course, be parallel with the base of the figure within the limits of random sampling if the population of 8-months milk production for the given age is the same irrespective of the age at which the subsequent lactation was made.

The curve for the mean eight-months milk production of the two-year-old group (the top curve of figure 6) is as close to a straight line parallel with the base of the figure as could well be expected. At no place is there more than 65-pound divergence from such a line. This divergence is seen in table 11 to be only slightly over the probable error of the mean production.

The curve for the three-year-old group is more variable than the two-year group due no doubt to the numbers on which it is based being less. The curve on the whole has a slight tendency upward as we progress from left to right. It is doubtful if this general trend is significant in comparison with the probable errors of the constants. Taken at its face value, however, it would indicate that the cows with a lactation record at 10 years of age would have had in general a slightly better record at three years old than would the general three-year-old group. That is, the cows of the three-year-old group were culled slightly so that the cows kept for milk production were somewhat better cows than the average run of three-year-olds.

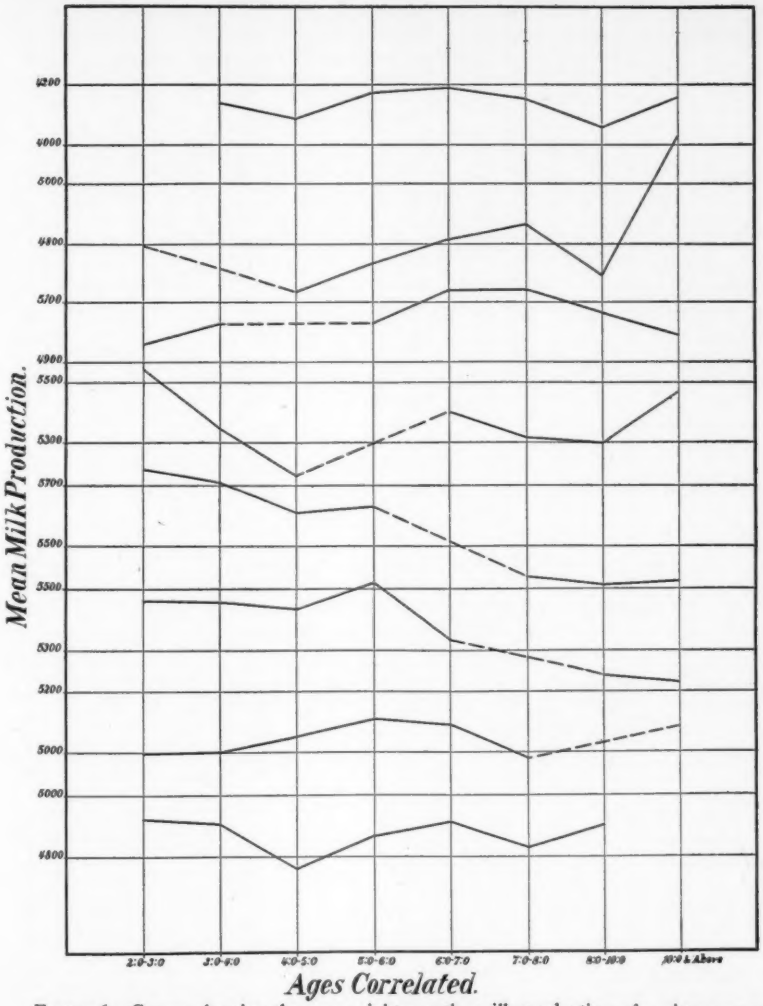


FIGURE 6.—Curves showing the mean eight-months milk production of a given age at each successive age with which the given age is correlated. The ordinates are the pounds of milk produced and the abscissae are the ages of the groups with which the given age is correlated. Proceeding from top to bottom of the figure the first line represents the mean milk production of the 2-year to 3-year group; the second the 3-year to 4-year group; the third the 4-year to 5-year; the fourth the 5-year to 6-year; the fifth the 6-year to 7-year; the sixth the 7-year to 8-year; the seventh the 8-year to 10-year, and the last the 10-year-and-older group. The lines obviously are quite irregular but in general do not diverge greatly from a line parallel with the base of the figure.

TABLE 12

*Correlation surface for amount of eight-months milk production at two years old and amount of eight-months milk production at five years old for pure-bred Jersey cows.*

| 2 years old \ 5 years old | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | 9000-9500 | 9500-10000 | 10000-10500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | 1 | | | | | | | | | | | | | | | 1 |
| 2500-3000 | | 1 | 2 | | | 2 | | | | | | | | | | 5 |
| 3000-3500 | 1 | 5 | 6 | 9 | 2 | 2 | 1 | 1 | | | | | | | | 27 |
| 3500-4000 | 2 | 2 | 4 | 3 | 6 | 3 | | 1 | | 2 | | | | | | 23 |
| 4000-4500 | 1 | 2 | | 8 | 9 | 4 | 5 | 3 | 1 | 1 | 2 | | | | | 36 |
| 4500-5000 | 1 | | | 3 | 5 | 3 | 4 | 6 | 4 | 2 | | | | | 1 | 29 |
| 5000-5500 | 1 | | | | 1 | 1 | 3 | 2 | 4 | | | | | | | 12 |
| 5500-6000 | | | | | 1 | | 1 | 1 | 1 | 1 | | | | | | 5 |
| 6000-6500 | | | | | | | | | 1 | | 1 | | | | | 2 |
| Total | 7 | 10 | 12 | 23 | 24 | 15 | 14 | 14 | 11 | 6 | 3 | 0 | 0 | 0 | 1 | 140 |

TABLE 13

*Correlation surface for amount of eight-months milk production at two years old and amount of eight-months milk production at six years old for pure-bred Jersey cows.*

| 2 years old \ 6 years old | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | 9000-9500 | 9500-10000 | 10000-10500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | | 1 | | | | 1 | | | | 1 | | | | | | | 1 |
| 2500-3000 | | 1 | 2 | 1 | | 1 | | | | 1 | | | | | | | 6 |
| 3000-3500 | | 1 | 5 | 5 | 5 | 1 | 2 | 2 | 1 | | | | | | | | 22 |
| 3500-4000 | | 1 | 1 | 4 | 2 | 1 | 3 | 3 | 2 | | | | | | | | 17 |
| 4000-4500 | | 1 | 1 | | 1 | 7 | 7 | 5 | 2 | 5 | | 3 | | | | | 32 |
| 4500-5000 | | | | | 4 | 5 | 4 | 5 | 1 | 4 | 2 | | | 1 | | | 26 |
| 5000-5500 | 1 | | | 1 | | | 2 | 1 | 3 | 1 | 1 | 1 | 1 | | 1 | | 13 |
| 5500-6000 | | | | | | | | 1 | | 1 | | | | | | 1 | 3 |
| 6000-6500 | | | | | | | | | | 1 | 1 | | | | | | 2 |
| Total | 1 | 5 | 9 | 11 | 12 | 15 | 18 | 17 | 9 | 13 | 4 | 4 | 1 | 1 | 1 | 1 | 122 |

TABLE 14

*Correlation surface for amount of eight-months milk production at two years old and amount of eight-months milk production at seven years old for pure-bred Jersey cows.*

| 2 years old \ 7 years old | 2000-2500 | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | | | 1 | | | | | | | | | | | | 1 |
| 2500-3000 | | | | 1 | 1 | 2 | | | | | | | | | 4 |
| 3000-3500 | 1 | | 1 | 5 | 2 | 4 | 4 | | | 2 | | | | | 19 |
| 3500-4000 | | | | 1 | 1 | 3 | 3 | 2 | 1 | 2 | | | | | 13 |
| 4000-4500 | | | 1 | 1 | 1 | 4 | 9 | 3 | 4 | 2 | | 1 | | | 26 |
| 4500-5000 | | | | | 1 | | | 3 | 3 | 5 | | | 1 | 1 | 14 |
| 5000-5500 | | | | | | | 2 | 2 | 1 | | 3 | | | | 8 |
| 5500-6000 | | | | | | | 2 | | 1 | | | | 1 | | 4 |
| 6000-6500 | | | | | | | | | | 1 | 1 | | | | 2 |
| Total | 1 | 0 | 3 | 8 | 6 | 13 | 20 | 10 | 10 | 12 | 4 | 1 | 2 | 1 | 91 |

TABLE 15

*Correlation surface for amount of eight-months milk production at two years old and amount of eight-months milk production at eight and nine years old for pure-bred Jersey cows.*

| 2 years old \ 8 and 9 years old | 2000-2500 | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | 9000-9500 | 10000-10500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | | 1 | | 1 | | | | | | | | | | | | | 2 |
| 2500-3000 | | | | 4 | 1 | | 2 | | | | | | | | | | 7 |
| 3000-3500 | 1 | 1 | 1 | 6 | 4 | | 1 | 2 | | 1 | | | | | | | 17 |
| 3500-4000 | | 1 | 1 | 1 | 2 | 3 | 6 | 3 | 4 | | | | | | | | 21 |
| 4000-4500 | | | 1 | 4 | 5 | 3 | 6 | 5 | 2 | 4 | 2 | | | | | | 32 |
| 4500-5000 | 1 | | | | | 7 | 3 | | 3 | 3 | 2 | | | | | | 19 |
| 5000-5500 | | | | | | | 4 | 2 | 1 | 1 | | | | | | 1 | 9 |
| 5500-6000 | | | | | | | | | 1 | | 1 | | | | | | 2 |
| Total | 2 | 3 | 3 | 16 | 12 | 13 | 22 | 12 | 11 | 9 | 5 | 0 | 0 | 0 | 0 | 1 | 100 |

The four-year- and five-year-old records are practically linear and parallel with the base. No selection has taken place in these cows to weed out the poor milkers.

The six- and seven-year curves both appear linear but have a downward tendency which looks significant when compared with its prob-

able errors. Thus in the six-year group the difference is $371.3 \pm 107.9$ or 3.4 times its probable error. Furthermore the drop in the value of the milk production of the six-year group is quite sudden, occurring with those cows which lactate in their seventh year and older. Selection can-

TABLE 16

*Correlation surface for amount of eight-months milk production at two years old and amount of eight-months milk production at ten years and older for pure-bred Jersey cows.*

| 2 years old \ 10 years old and older | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2500-3000 | 1 | | | | 1 | | | | | | | 2 |
| 3000-3500 | | 1 | | 2 | 1 | 1 | | | | | | 5 |
| 3500-4000 | | 1 | | 1 | | 1 | | | | | | 3 |
| 4000-4500 | | 2 | 2 | 5 | 5 | 3 | 3 | | 1 | | 1 | 22 |
| 4500-5000 | | | | | | 3 | | 2 | | | | 5 |
| 5000-5500 | | | | | | | | | 2 | | | 2 |
| 5500-6000 | | | | | | | | | 1 | | | 1 |
| Total | 1 | 4 | 2 | 8 | 7 | 8 | 3 | 2 | 4 | 0 | 1 | 40 |

TABLE 17

*Correlation surface for amount of eight-months milk production at three years old and amount of eight-months milk production at four years old for pure-bred Jersey cows.*

| 3 years old \ 4 years old | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | | 1 | | | | | 1 | | | | | | | 1 |
| 2500-3000 | 1 | | 1 | 1 | | | 1 | | | | | | | 4 |
| 3000-3500 | | 3 | 4 | 3 | 2 | 1 | | | | | | | | 13 |
| 3500-4000 | | 2 | 3 | 9 | 5 | 4 | 1 | | | | | | | 24 |
| 4000-4500 | | 4 | 2 | 7 | 9 | 10 | 1 | 1 | | 1 | | | 1 | 36 |
| 4500-5000 | | | 1 | 6 | 4 | 7 | 5 | 2 | 2 | | | | | 27 |
| 5000-5500 | | 1 | | 1 | 5 | 6 | 2 | 2 | 2 | | | | | 19 |
| 5500-6000 | | | | | 3 | 2 | 2 | 2 | 1 | 1 | | | | 11 |
| 6000-6500 | | | | | 1 | 2 | 2 | | 2 | 1 | | | | 8 |
| 6500-7000 | | | | | | | | 3 | 1 | 1 | | | | 5 |
| 7000-7500 | | | | 1 | | | | | 1 | | 1 | 1 | | 4 |
| 7500-8000 | | | | | | | | | | | 1 | | | 1 |
| Total | 1 | 11 | 11 | 28 | 29 | 32 | 14 | 10 | 9 | 4 | 2 | 1 | 1 | 153 |

not account for this drop for it goes directly opposite to the direction in which selection would be made unless the highly unlikely assumption is made that the cows with high six-year-old records die before their seventh lactation. This assumption is known not to be true as the records of death are accurately kept. The history of the herd is accurately known and while perhaps a half a dozen old cows purchased at its beginning their production was fair and they were of ages 6 and older with no centering on any age. No other possible reason for the drop is known to the author. The reason for this drop consequently remains obscure.

The curves for the eight-and-nine-year and the ten-and-above groups all appear linear and parallel with the base, indicating that no selection had been practiced in choosing these animals.

To sum up the results of this study, no clear evidence of selection of animals to be kept as further milk producers is evidenced by the mean milk production of any age in comparison with the other lactations that the cow was known to be milking.

TABLE 18

*Correlation surface for amount of eight-months milk production at three years old and amount of eight-months milk production at five years old for pure-bred Jersey cows.*

| 3 years old \ 5 years old | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | 9000-9500 | 9500-10000 | 10000-10500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | 1 | | | | | | | | | | | | | | | 1 |
| 2500-3000 | 2 | | | | 1 | 1 | | | 1 | | | | | | | 5 |
| 3000-3500 | 3 | 3 | 5 | 3 | 2 | 1 | | | | | | | | | | 17 |
| 3500-4000 | 1 | 4 | 2 | 6 | 1 | | 1 | | | 1 | | | | | | 16 |
| 4000-4500 | | 5 | 4 | 6 | 5 | 1 | | 1 | | | | | | | | 22 |
| 4500-5000 | 1 | 1 | 4 | 5 | 5 | 6 | 3 | | 1 | 1 | | | | | | 27 |
| 5000-5500 | 1 | | 1 | 2 | 6 | 1 | 2 | 4 | 3 | | | | | | 1 | 21 |
| 5500-6000 | 1 | | | 1 | 1 | 4 | 1 | 1 | 2 | 1 | | | | | | 12 |
| 6000-6500 | | | | 1 | 1 | 3 | | 5 | 2 | 1 | | | | | | 13 |
| 6500-7000 | | | | | | 1 | 1 | | 1 | | | | | | | 3 |
| 7000-7500 | | | | | | | 1 | 1 | 2 | | 1 | | | | | 5 |
| 7500-8000 | | | | | | | | | | | 1 | | | | | 1 |
| Total | 10 | 13 | 16 | 24 | 22 | 18 | 9 | 12 | 12 | 4 | 2 | 0 | 0 | 0 | 1 | 143 |

TABLE 19

*Correlation surface for amount of eight-months milk production at three years old and amount of eight-months milk production at six years old for pure-bred Jersey cows.*

| 3 years old \ 6 years old | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | 9000-9500 | 9500-10000 | 10000-10500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | | | | | | 1 | | | | | | | | | | | 1 |
| 2500-3000 | 1 | | | | 1 | | 1 | | | | | | | | | | 3 |
| 3000-3500 | | 2 | 2 | 5 | 1 | 3 | 1 | | | | | | | | | | 14 |
| 3500-4000 | | 1 | 4 | 1 | 2 | 2 | | | 1 | 1 | | | | | | | 12 |
| 4000-4500 | | | 2 | 1 | 3 | 3 | 3 | 1 | | | | | | | | 1 | 14 |
| 4500-5000 | | | | 2 | 1 | 2 | 3 | 7 | 3 | 2 | | 1 | | | | | 21 |
| 5000-5500 | 1 | | | | 2 | 4 | 5 | 4 | 1 | 3 | 2 | | | | | | 22 |
| 5500-6000 | | | | 1 | 1 | | 2 | 2 | | 1 | | | | 1 | 1 | | 9 |
| 6000-6500 | | | | | 1 | 2 | 1 | 2 | 2 | | | 2 | | | | | 10 |
| 6500-7000 | | | | | | 1 | | | | 1 | 1 | | | | | | 3 |
| 7000-7500 | | | | | | | 1 | | 1 | 1 | 2 | | | | | | 5 |
| 7500-8000 | | | | | | | | | | | 1 | | | | | | 1 |
| Total | 2 | 3 | 8 | 10 | 12 | 18 | 17 | 16 | 8 | 9 | 6 | 3 | 0 | 1 | 1 | 1 | 115 |

*The standard deviations of milk production as influenced by the length of time the cow is retained in the herd*

A similar analysis for the effect of selection of cows at a given age on the basis of their milk production to be retained as milkers in after years is given in table 20. The arrangement of the data is entirely similar to that of table 11. The vertical columns give the standard deviations (without SHEPPARD'S correction) for the age of the cows indicated; the values are, from top to bottom, those of the given year when the same-age cows also have other records at the years indicated on the

TABLE 20

*Standard deviations of milk production of a given year when correlated with other given years.*

| Age | 2 years | 3 years | 4 years | 5 years |
|---|---|---|---|---|
| 2 to 3 | | 1109.14 ± 39.00 | 1166.17 ± 42.17 | 1306.56 ± 52.67 |
| 3 to 4 | 806.99 ± 28.37 | | 1103.81 ± 42.56 | 1427.69 ± 56.94 |
| 4 to 5 | 736.58 ± 26.63 | 1055.55 ± 40.70 | | 1195.11 ± 47.66 |
| 5 to 6 | 782.79 ± 31.55 | 1136.60 ± 45.33 | 1047.07 ± 41.76 | |
| 6 to 7 | 797.53 ± 34.44 | 1157.00 ± 51.45 | 1103.37 ± 48.04 | 1251.05 ± 54.02 |
| 7 to 8 | 831.76 ± 41.59 | 1137.94 ± 54.83 | 1027.18 ± 46.09 | 1109.12 ± 46.57 |
| 8 to 10 | 744.36 ± 34.00 | 1147.04 ± 53.13 | 1020.66 ± 43.89 | 1243.36 ± 49.25 |
| 10 and older | 621.36 ± 46.86 | 1290.28 ± 141.18 | 1074.39 ± 73.20 | 1174.59 ± 75.54 |

TABLE 20 (continued)

*Standard deviations of milk production of a given year when correlated with other given years.*

| Age | 6 years | 7 years | 8 and 9 years | 10 and older |
|---|---|---|---|---|
| 2 to 3 | 1453.51 ± 62.76 | 1222.82 ± 61.14 | 1255.63 ± 81.12 | 1121.10 ± 84.54 |
| 3 to 4 | 1417.51 ± 63.04 | 1281.58 ± 61.75 | 1390.96 ± 64.43 | 932.63 ± 102.05 |
| 4 to 5 | 1699.38 ± 73.99 | 1262.45 ± 56.65 | 1285.72 ± 55.29 | 1052.16 ± 71.68 |
| 5 to 6 | 1362.64 ± 58.84 | 1235.78 ± 51.89 | 1355.07 ± 53.67 | 1198.34 ± 77.07 |
| 6 to 7 | | 1288.48 ± 55.19 | 1293.65 ± 50.69 | 1004.11 ± 59.87 |
| 7 to 8 | 1274.72 ± 54.60 | | 1355.50 ± 52.61 | 1093.68 ± 60.63 |
| 8 to 10 | 1236.58 ± 48.47 | 1159.80 ± 45.01 | | 1141.55 ± 48.89 |
| 10 and older | 1108.36 ± 66.08 | 1061.13 ± 58.83 | 1149.98 ± 49.25 | |

left margin of the table. The data for the calculation of these constants are taken from correlation tables 9 to 40.

These data are graphically represented in figure 7, the values of the standard deviations being represented as ordinates and the ages at which the cows had another lactation as the abscissae. The curves progressing from top to bottom of the figure are for the lactation at the 2, 3, 4, 5, 6, 7, 8-and-9 and 10-and-older groups. The lines generated by those curves should, of course, be parallel with the base if there has been no selection practiced. If selection has been at any given place it should be expected to curtail the low-producing cows and thus reduce the standard deviation of the population as a whole.

TABLE 21

*Correlation surface for amount of eight-months milk production at three years old and amount of eight-months milk production at seven years old for pure-bred Jersey cows.*

| 3 years old \ 7 years old | 2000-2500 | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2500-3000 | | 1 | | | | | | | | | | | | | 1 |
| 3000-3500 | 1 | | 2 | 1 | 1 | 2 | 3 | | | | | | | | 10 |
| 3500-4000 | | | 2 | 3 | 4 | 2 | 1 | 1 | | 1 | | | | 1 | 15 |
| 4000-4500 | | | | 3 | 1 | 3 | 1 | 2 | 1 | 1 | 1 | | | | 13 |
| 4500-5000 | | | | | 2 | 4 | 4 | 1 | 4 | 3 | | | 1 | | 19 |
| 5000-5500 | | | | | 2 | 2 | 2 | 2 | 2 | 2 | 2 | | 1 | | 15 |
| 5500-6000 | | | | | | | 1 | | 2 | 1 | | 1 | | | 5 |
| 6000-6500 | | | | | | | 4 | 1 | 3 | 3 | | | | | 11 |
| 6500-7000 | | | | | | | 1 | 2 | | 1 | | | | | 4 |
| 7000-7500 | | | | | | | | | 1 | | 3 | | | | 4 |
| 7500-8000 | | | | | | | | | | 1 | | | | | 1 |
| Total | 1 | 1 | 4 | 7 | 10 | 13 | 17 | 9 | 13 | 13 | 6 | 1 | 2 | 1 | 98 |

TABLE 22

*Correlation surface for amount of eight-months milk production at three years old and amount of eight-months milk production at eight and nine years old for pure-bred Jersey cows.*

| 3 years old \ 8 and 9 years old | 2000-2500 | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | 9000-9500 | 9500-10000 | 10000-10500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2500-3000 | | 1 | 1 | | | 2 | | | 1 | 1 | | | | | | | | 6 |
| 3000-3500 | 1 | 2 | 3 | 3 | | 1 | 2 | 1 | 2 | | | | | | | | | 15 |
| 3500-4000 | | 1 | 2 | 3 | 3 | 2 | 2 | | | | | | | | | | | 13 |
| 4000-4500 | | | | 3 | 1 | 1 | 2 | 1 | 1 | | 1 | | | | | | | 10 |
| 4500-5000 | | | 1 | 2 | 2 | 5 | 5 | 2 | 1 | | | | | | | | | 18 |
| 5000-5500 | | | | 1 | 2 | 2 | 6 | 2 | 5 | 1 | | 1 | | | | | | 20 |
| 5500-6000 | | | | | 2 | 1 | | | 2 | | | | | | | | 1 | 6 |
| 6000-6500 | | | | | 2 | 1 | 2 | 2 | 2 | 1 | 2 | | | | | | | 12 |
| 6500-7000 | | | | | | | 1 | | | 1 | 2 | | | | | | | 4 |
| 7000-7500 | | | | | | | | | | | | 1 | | | | 1 | | 2 |
| Total | 1 | 4 | 7 | 12 | 12 | 15 | 20 | 8 | 14 | 4 | 5 | 2 | 0 | 0 | 0 | 1 | 1 | 106 |

The curves for the two, three, four, five, seven, eight-and-nine and ten-and-older age groups are obviously linear and follow a general course parallel with the base. The standard deviations for each of these given ages are therefore constant to all intents and purposes. Since one effect of selection is to reduce the standard deviation of the selected race in

TABLE 23

*Correlation surface for amount of eight-months milk production at three years old and amount of eight-months milk production at ten years and older for pure-bred Jersey cows.*

| 10-and-above years old \ 3 years old | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 3000-3500 | 1 | 1 | | | | | | | | | 2 |
| 3500-4000 | | | | | | | | | | | 0 |
| 4000-4500 | | | 1 | | | 1 | 1 | 1 | 1 | | 5 |
| 4500-5000 | | 1 | 1 | | | 1 | | | | | 3 |
| 5000-5500 | | | | 1 | | 2 | 1 | 1 | | | 5 |
| 5500-6000 | | | | | | 1 | | 1 | | | 2 |
| 6000-6500 | | | | | | | | | | | 0 |
| 6500-7000 | | | | | | | | | 1 | 1 | 2 |
| Total | 1 | 2 | 2 | 1 | 0 | 5 | 2 | 3 | 2 | 1 | 19 |

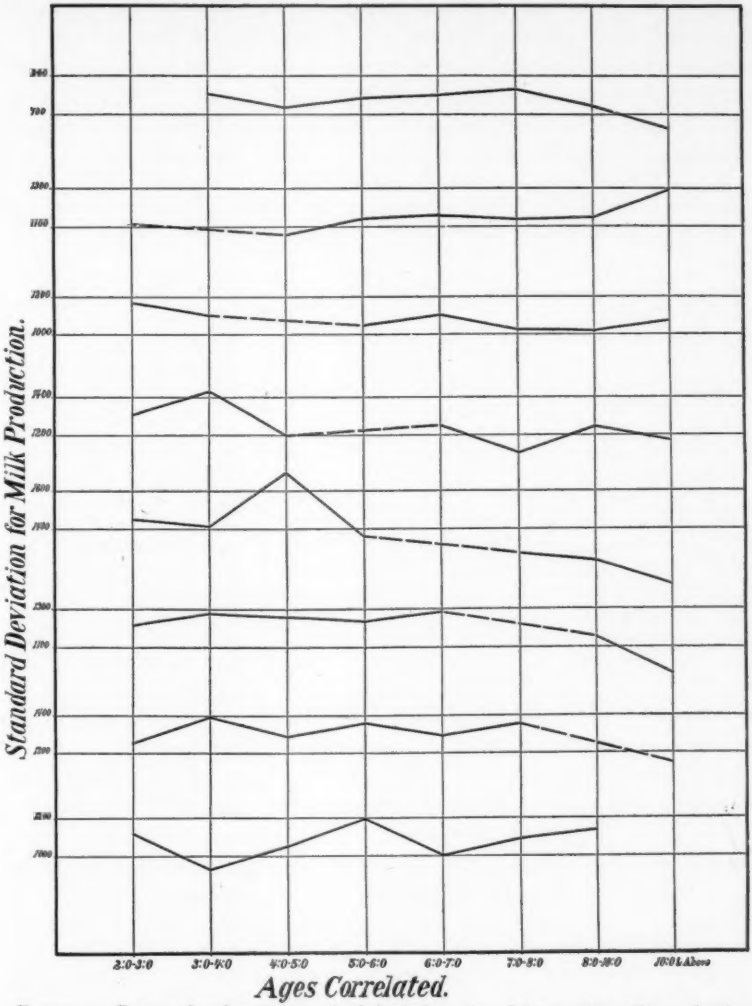


FIGURE 7.—Curves showing the standard deviations for eight-months milk production of a given age in the cow's life at the successive ages with which the given age is correlated. The ordinates are the standard deviations for the pounds of milk produced. The abscissae are the ages of the groups with which the given age is correlated and for which the given age had the standard deviation plotted. Proceeding from top to bottom the curves show the standard deviation for the 2, 3, 4, 5, 6, 7, 8-and-9 and 10-year-and-older age groups. The lines are quite regular and in general are parallel with the base as would be expected if no selection were practiced.

comparison with that of the unselected race, it follows that no selection is evidenced in these age groups. The case for the six-year group is not so clear. Here the general trend of the curve seems downward. This downward trend is only slight as compared with its probable error. The reason for it is as obscure as in the similar trend of the mean-8-months-production curve.

TABLE 24

*Correlation surface for amount of eight-months milk production at four years old and amount of eight-months milk production at five years old for pure-bred Jersey cows.*

| 5 years old \ 4 years old | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 3000-3500 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | | | | | | 8 |
| 3500-4000 | | 1 | 6 | 5 | 1 | 3 | | 1 | | | | | 17 |
| 4000-4500 | | 3 | 5 | 2 | 3 | 2 | 1 | | | | 1 | | 17 |
| 4500-5000 | | | 4 | 8 | 6 | 6 | 2 | 1 | 2 | | | | 29 |
| 5000-5500 | | | 1 | 3 | 6 | 9 | 4 | | 1 | | | | 24 |
| 5500-6000 | | | 1 | 2 | | 4 | 2 | 2 | | | | | 11 |
| 6000-6500 | | | | 2 | 2 | 2 | 3 | 3 | | 2 | | | 14 |
| 6500-7000 | | | | | 2 | 2 | 2 | | 3 | 1 | | | 10 |
| 7000-7500 | | | | 1 | 1 | 1 | | 1 | 2 | | 1 | | 7 |
| 7500-8000 | | | | | | 1 | 2 | | 1 | | | | 4 |
| 8000-8500 | | | | | | | 1 | | | | | 1 | 2 |
| Total | 1 | 5 | 18 | 25 | 22 | 31 | 18 | 8 | 9 | 3 | 2 | 1 | 143 |

The general conclusion indicated by these data is that no selection of the high-producing cows to retain only the high milker in the older ages based on their earlier-recorded production has been practiced.

### *The coefficients of variation of milk production as influenced by the time the cow is retained in the herd*

The relative measure of the effect of any change which may have occurred is given by the coefficients of variation for the milk production of any given age. The constants for this comparison are given in table 25. The arrangement of them in this table is identical with that for tables 11 and 20. The age for which the coefficients of variation are determined is given above the columns. The ages at which the cows have records at other ages are given on the left. The data for these are calculated from correlation tables 9 to 40.

TABLE 25

*Coefficients of variation of milk production of a given year when correlated with other given years.*

| Age | 2 years | 3 years | 4 years | 5 years |
|---|---|---|---|---|
| 2 to 3 | | 23.13 ± .85 | 23.50 ± .87 | 23.57 ± 1.02 |
| 3 to 4 | 19.49 ± .69 | | 21.94 ± .89 | 26.71 ± 1.15 |
| 4 to 5 | 18.00 ± .67 | 22.74 ± .93 | | 23.02 ± .96 |
| 5 to 6 | 18.73 ± .79 | 23.98 ± 1.01 | 20.80 ± .87 | |
| 6 to 7 | 19.02 ± .85 | 24.01 ± 1.13 | 21.46 ± .95 | 23.16 ± 1.04 |
| 7 to 8 | 20.01 ± 1.04 | 23.38 ± 1.17 | 19.97 ± .93 | 20.86 ± .92 |
| 8 to 10 | 18.33 ± .85 | 24.42 ± 1.17 | 20.14 ± .89 | 23.39 ± .96 |
| 10 and older | 14.93 ± 1.16 | 24.95 ± 2.90 | 21.51 ± 1.57 | 21.48 ± 1.41 |

TABLE 25 (continued)

*Coefficients of variation of milk production of a given year when correlated with other given years.*

| Age | 6 years | 7 years | 8 and 9 years | 10 years and older |
|---|---|---|---|---|
| 2 to 3 | 25.26 ± 1.14 | 22.38 ± 1.15 | 24.65 ± 1.21 | 22.76 ± 1.82 |
| 3 to 4 | 24.82 ± 1.18 | 23.48 ± 1.17 | 27.28 ± 1.34 | 19.00 ± 2.15 |
| 4 to 5 | 30.28 ± 1.42 | 23.72 ± 1.09 | 24.95 ± 1.14 | 22.10 ± 1.57 |
| 5 to 6 | 24.20 ± 1.09 | 22.38 ± .97 | 26.02 ± 1.10 | 24.62 ± 1.71 |
| 6 to 7 | | 24.15 ± 1.09 | 24.02 ± 1.04 | 20.43 ± 1.24 |
| 7 to 8 | 23.61 ± 1.09 | | 26.68 ± 1.12 | 22.64 ± 1.34 |
| 8 to 10 | 23.02 ± .95 | 22.22 ± .89 | | 23.28 ± 1.04 |
| 10 and older | 20.59 ± 1.31 | 20.42 ± 1.15 | 22.18 ± .99 | |

To facilitate comparison of the constants for one age with those of another age the values of the coefficients are represented as curves in figure 8. The arrangement of these curves is entirely similar to that of figures 6 and 7.

The values of the coefficients of variation are represented as ordinates and the ages at which the cows had another lactation as abscissae. The curves progressing from top to bottom of the figure are for ages 2, 3, 4, 5, 6, 7, 8 and 9, and 10 and above. The same reasoning, that if no selection of animals based on their records of previous years has taken place the curves generated by these coefficients of variation should be straight lines parallel with the base, still holds.

The curves in figure 8 are individually somewhat more irregular than the curves for the mean milk production of a given age (figure 6) and the standard deviations of a given age (figure 7). No definite trend of the coefficients either toward a higher value or toward a lower value is seen in the coefficients except those for the six-year period. This six-

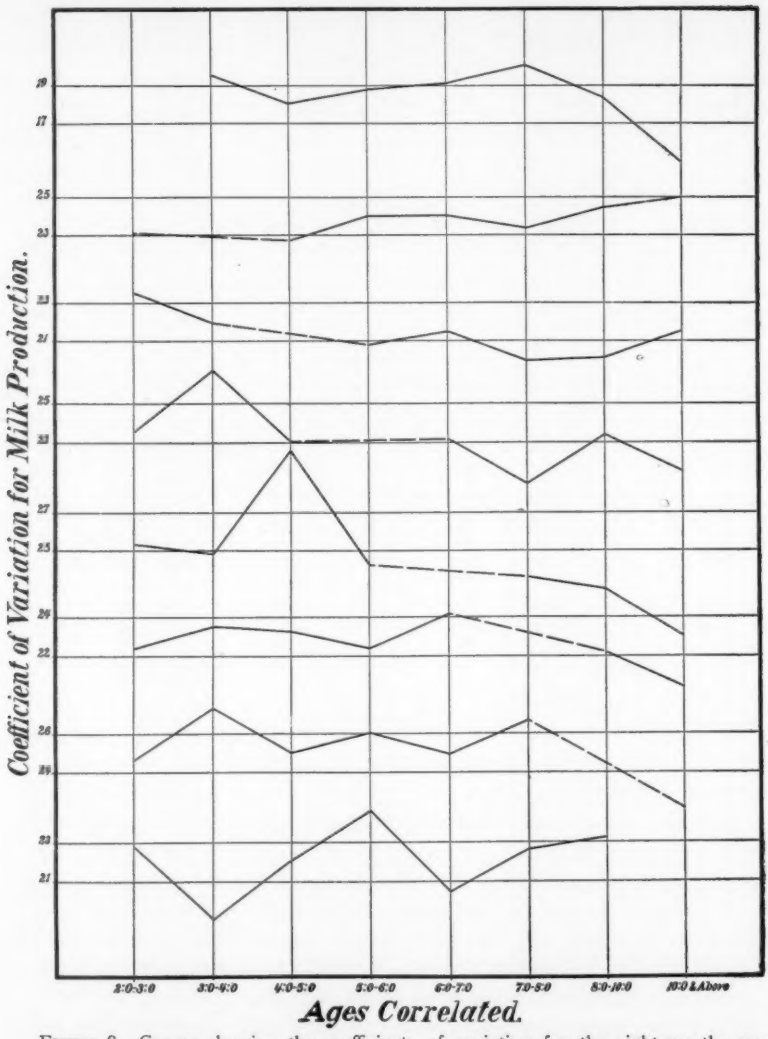


FIGURE 8.—Curves showing the coefficients of variation for the eight-months production of a given age at each successive age with which the milk yield of the given age is correlated. The ordinates are the coefficients of variation and the abscissae are the ages of the groups with which the given age is correlated. The significance of the curves proceeding from top to bottom is the same as in figures 6 and 7. The lines generated by the curves should, of course, as in the preceding case be parallel with the base and linear if no effect of selection of cattle based on their previous records has taken place.

TABLE 26

*Correlation surface for amount of eight-months milk production at four years old and amount of eight-months milk production at six years old for pure-bred Jersey cows.*

| 6 years old \ 4 years old | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2500-3000 | 1 | | | | | | | 1 | | | | | | 2 |
| 3000-3500 | | 1 | | 2 | | 1 | | | | | | | | 4 |
| 3500-4000 | | 1 | 4 | 3 | | 1 | | | | | | | | 9 |
| 4000-4500 | | | 3 | 4 | 1 | 2 | | | | | | | | 10 |
| 4500-5000 | | | 2 | 3 | 6 | 2 | 1 | | 1 | | | | | 15 |
| 5000-5500 | | 2 | 1 | 3 | 2 | 4 | 2 | 1 | | 1 | | | | 16 |
| 5500-6000 | | 1 | | 2 | 4 | 4 | 2 | 1 | 1 | 1 | 1 | | | 17 |
| 6000-6500 | | | | 2 | 4 | 6 | 6 | 3 | 1 | 1 | | | | 23 |
| 6500-7000 | | | | 1 | 1 | 1 | 2 | | 1 | 1 | 1 | | | 8 |
| 7000-7500 | | | | 1 | 2 | 1 | 1 | | 1 | | | | | 6 |
| 7500-8000 | | | | | | 1 | | | 3 | | | | | 4 |
| 8000-8500 | | | | | | | 1 | 1 | 1 | | | | | 3 |
| 8500-9000 | | | | | | | | | | | | | | 0 |
| 9000-9500 | | | | | | 1 | | 1 | | | | | | 2 |
| 9500-10000 | | | | | | | | | | | | | | 0 |
| 10000-10500 | | | | | | | | | | | | | 1 | 1 |
| Total | 1 | 5 | 10 | 21 | 20 | 24 | 15 | 8 | 9 | 4 | 2 | 0 | 1 | 120 |

TABLE 27

*Correlation surface for amount of eight-months milk production at four years old and amount of eight-months milk production at seven years old for pure-bred Jersey cows.*

| 7 years old \ 4 years old | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500017000 | 7000-7500 | 7500-8000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | | 1 | | | | | | | | | | 1 |
| 2500-3000 | 1 | | | | | | | | | | | 1 |
| 3000-3500 | | | 1 | 2 | 1 | | | | | | | 4 |
| 3500-4000 | | 1 | 2 | 4 | 2 | 1 | | | | | | 10 |
| 4000-4500 | | | | 5 | 2 | 2 | 1 | | | | | 10 |
| 4500-5000 | | | 5 | 4 | 3 | 3 | | | | | | 15 |
| 5000-6000 | | | 2 | 2 | 2 | 6 | 3 | 3 | 1 | | | 19 |
| 5500-6000 | | | | 1 | 7 | 4 | 2 | 2 | | 1 | | 17 |
| 6000-6500 | | | | 2 | 3 | 1 | 3 | 3 | 1 | 1 | | 14 |
| 6500-7000 | | | | | 2 | 3 | | | 3 | 2 | | 10 |
| 7000-7500 | | | | | | | 1 | 1 | 1 | 2 | 1 | 6 |
| 7500-8000 | | | | | | | 1 | | 1 | | | 2 |
| 8000-8500 | | | | | | 2 | 1 | | | | | 3 |
| 8500-9000 | | | | | | | 1 | | | | | 1 |
| Total | 1 | 2 | 10 | 20 | 22 | 22 | 13 | 9 | 7 | 6 | 1 | 113 |

year curve is quite irregular. The general tendency is slightly downward indicating if it proves significant some selection on the basis of the

TABLE 28

*Correlation surface for amount of eight-months milk production at four years old and amount of eight-months milk production at eight and nine years old for pure-bred Jersey cows.*

| 4 years old \ 8 and 9 years old | 2000-2500 | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | 9000-9500 | 9500-10000 | 10000-10500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2500-3000 | | 1 | 1 | | | | | | | | | | | | | | | 2 |
| 3000-3500 | | | | 1 | | | | | | | | | | | | | | 1 |
| 3500-4000 | | | 2 | 3 | 1 | 2 | 3 | 1 | | | | | | | | | | 12 |
| 4000-4500 | 2 | | 2 | 2 | 5 | 3 | 6 | | 4 | 2 | | | | | | | | 26 |
| 4500-5000 | | | 1 | 1 | 5 | 3 | 8 | 1 | 1 | 3 | 2 | | | | | | | 25 |
| 5000-5500 | | | 4 | 2 | | 2 | 4 | 1 | 2 | 1 | 1 | | | | | | | 17 |
| 5500-6000 | | | | | 2 | 4 | 4 | 2 | | 4 | | 1 | 1 | | | | | 18 |
| 6000-6500 | | | | | | 2 | 3 | 3 | | 1 | 1 | | | | | | | 10 |
| 6500-7000 | | | | | 2 | | 1 | 2 | | | | | | | | | 1 | 6 |
| 7000-7500 | | | | | | | 2 | | | 1 | 1 | | | | | | | 4 |
| 7500-8000 | | | | | | | | 1 | | | 1 | | | | | | | 2 |
| Total | 2 | 1 | 10 | 9 | 15 | 16 | 31 | 11 | 7 | 12 | 6 | 1 | 1 | 0 | 0 | 0 | 1 | 123 |

TABLE 29

*Correlation surface for amount of eight-months milk production at four years old and amount of eight-months milk production at ten years and older for pure-bred Jersey cows.*

| 10-and-above years old \ 4 years old | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | | | | 1 | | | | | | | 1 |
| 2500-3000 | | | | | | 1 | | | | | 1 |
| 3000-3500 | 1 | 1 | 1 | 2 | | | | | | | 5 |
| 3500-4000 | | | | 1 | | 1 | 1 | | | | 3 |
| 4000-4500 | | | 1 | 3 | 3 | 1 | 1 | 1 | | 1 | 11 |
| 4500-5000 | | | 1 | 1 | | 2 | | | | 2 | 6 |
| 5000-5500 | | 1 | | 1 | 3 | 3 | 2 | | | 1 | 11 |
| 5500-6000 | | | | | 2 | | 1 | | 1 | 1 | 5 |
| 6000-6500 | | | | 1 | 1 | 2 | | | | | 4 |
| 6500-7000 | | | | 1 | | | | | | | 1 |
| 7000-7500 | | | | 1 | | | | | | | 1 |
| Total | 1 | 2 | 3 | 12 | 9 | 10 | 5 | 1 | 1 | 5 | 49 |

six-year milk production. Neglecting the rise at four years as obviously extraneous to the general trend of the curve, the difference between the six-year coefficients of variation for cows which were milked at 2 years and the six-year coefficients of variation for cows which were milked at 10 years is $4.67 \pm 1.74$, or the divergence is 2.7 times its probable error. The difference is therefore doubtfully significant, in fact probably not significant.

The conclusion which may be derived from these data is that no effect of selection of cows on the basis of their milk records is manifested by the coefficients of variation for any given age taken in conjunction with the length of time the cows remain as milkers in the herd.

TABLE 30

*Correlation surface for amount of eight-months milk production at five years old and amount of eight-months milk production at six years old for pure-bred Jersey cows.*

| 6 years old \ 5 years old | 3000-3500 | 3500 4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2500-3000 | 1 | 1 | | | | | | | | | | | 2 |
| 3000-3500 | 2 | | | | | | | | | | | | 2 |
| 3500-4000 | | 4 | 3 | 2 | | | | | | | | | 9 |
| 4000-4500 | 2 | 4 | 2 | 5 | 1 | | | | | | | | 14 |
| 4500-5000 | 1 | | 1 | 4 | 5 | 3 | | | | | | | 14 |
| 5000-5500 | 1 | 2 | 1 | 4 | 5 | 4 | | 1 | 1 | | | | 19 |
| 5500-6000 | | 2 | 1 | 1 | 7 | 1 | 1 | 3 | 1 | | | | 17 |
| 6000-6500 | | | 1 | 1 | 3 | 2 | 5 | 3 | 1 | | | | 16 |
| 6500-7000 | | | | | 1 | 1 | 4 | 2 | | | | | 8 |
| 7000-7500 | | | | 1 | 1 | 1 | | 2 | 2 | 1 | 1 | 1 | 10 |
| 7500-8000 | | | | | | | | 2 | 3 | | 1 | | 6 |
| 8000-8500 | | | | | 1 | | | | 1 | | | | 2 |
| 8500-9000 | | | | | | | | | | | | | 0 |
| 9000-9500 | | | | | | 1 | | | 1 | | | | 2 |
| 9500-10000 | | | | | | | | | 1 | | | | 1 |
| Total | 7 | 13 | 9 | 18 | 24 | 13 | 10 | 13 | 11 | 1 | 2 | 1 | 122 |

Among the important general conclusions coming out of this study of the mean 8-months milk production, the standard deviation and coefficients of variation of this milk production within the different age groups determined separately for the other ages at which they had lactations in the herd, perhaps the most important is that the data for which the curve of mean milk production with age (figure 4) was obtained are free

TABLE 31

*Correlation surface for amount of eight-months milk production at five years old and amount of eight-months milk production at seven years old for pure-bred Jersey cows.*

| 7 years old \ 5 years old | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | | 1 | | | | | | | | | | 1 |
| 2500-3000 | 1 | | | | | | | | | | | 1 |
| 3000-3500 | 1 | 1 | | | | | | | | | | 2 |
| 3500-4000 | 1 | 1 | 1 | 2 | | 3 | 1 | | | | | 9 |
| 4000-4500 | 2 | 2 | 1 | 4 | 4 | | | | | | | 13 |
| 4500-5000 | | 2 | 6 | 4 | 5 | 3 | | 1 | | | | 21 |
| 5000-5500 | 2 | 2 | 2 | 4 | 5 | 4 | 1 | 2 | 1 | | | 23 |
| 5500-6000 | | | 1 | 2 | 4 | 2 | 2 | | | | | 11 |
| 6000-6500 | | | | 3 | 5 | 3 | 4 | 5 | 1 | | | 21 |
| 6500-7000 | | | 1 | 2 | 2 | 1 | 2 | 2 | | | 1 | 11 |
| 7000-7500 | | | | | | | 3 | 1 | 3 | | 1 | 8 |
| 7500-8000 | | 1 | | | 2 | 1 | | | | | | 4 |
| 8000-8500 | | | | | | 1 | 1 | | 1 | | | 3 |
| 8500-9000 | | | | | | | | | | 1 | | 1 |
| Total | 7 | 10 | 12 | 21 | 27 | 18 | 14 | 11 | 6 | 1 | 2 | 129 |

from any error due to selection of cows that were to remain in the herd on the basis of the records they made in their first, second or later lactations. From this it follows that the rise and fall of the curve for mean milk production with advancing age is due strictly to the physiological changes brought about in the mammary functions of the cow by age. The general equation to this physiological change expresses the law by which it is governed in the same way that MINOT (1891, 1907), LEWENZ and PEARSON (1904), DONALDSON (1908, 1909, 1910, 1911), HATAI (1911), and PEARL with the assistance of PEPPER (1907), have expressed the similar law for the manner in which the metabolic functions producing growth change with increasing age.

Added significance is given by this analysis to the conclusions previously indicated concerning the variation of milk within a given age, the correlation of age and milk production and the change of the variability of milk production with age.

TABLE 32

*Correlation surface for amount of eight-months milk production at five years old and amount of eight-months milk production at eight and nine years old for pure-bred Jersey cows.*

| 8 and 9 years old \ 5 years old | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | | 1 | | | | | | 1 | | | | | 2 |
| 2500-3000 | 2 | 1 | | | | 1 | | | | | | | 4 |
| 3000-3500 | 3 | 1 | 1 | | 1 | | | | | | | | 6 |
| 3500-4000 | 3 | 5 | 1 | 1 | 3 | | 2 | 1 | | | | | 16 |
| 4000-4500 | 2 | 2 | 4 | 4 | 4 | 3 | 1 | | | | | | 20 |
| 4500-5000 | 1 | | 2 | 2 | 7 | 3 | 1 | 1 | | | | | 17 |
| 5000-5500 | | | 4 | 4 | 4 | 4 | 2 | 1 | 1 | | | | 20 |
| 5500-6000 | | 2 | 3 | 2 | 4 | 3 | 2 | | 2 | | | | 18 |
| 6000-6500 | | 1 | 1 | 1 | 6 | 4 | 1 | 2 | 2 | 1 | 1 | | 20 |
| 6500-7000 | | | 1 | 1 | 1 | 1 | 3 | 4 | | | 2 | | 13 |
| 7000-7500 | | | | | | | 1 | | 2 | 1 | | | 4 |
| 7500-8000 | | | | 1 | | | | | | | | | 1 |
| 8000-8500 | | | | | | | | | | | 1 | 1 | 2 |
| 8500-9000 | | | | | | | | | | | | | 0 |
| 9000-9500 | | | | | | | | | | | | | 0 |
| 9500-10000 | | | | | | | 1 | | | | | | 1 |
| 10000-10500 | | | | | | 1 | | | | | | | 1 |
| Total | 11 | 13 | 17 | 16 | 30 | 20 | 14 | 10 | 7 | 2 | 4 | 1 | 145 |

TABLE 33

*Correlation surface for amount of eight-months milk production at five years old and amount of eight-months milk production at ten years and older for pure-bred Jersey cows.*

| 10 years and older \ 5 years old | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | | 1 | | | | | | | | | 1 |
| 2500-3000 | | 1 | | 1 | | | | | | | 2 |
| 3000-3500 | 2 | 1 | | 1 | 1 | | | | | | 5 |
| 3500-4000 | 1 | | | | 1 | | | 3 | | | 5 |
| 4000-4500 | | 1 | | 2 | 1 | 1 | 1 | | 1 | | 7 |
| 4500-5000 | | 1 | 2 | 1 | 1 | 2 | 2 | 1 | | | 10 |
| 5000-5500 | | | 3 | | 1 | 4 | 2 | 1 | | | 11 |
| 5500-6000 | | | 1 | | | 1 | 2 | 1 | | | 5 |
| 6000-6500 | | | | | 1 | | 1 | | | | 2 |
| 6500-7000 | | | | | | 1 | | | 3 | 1 | 5 |
| 7000-7500 | | | | | | | 1 | | | | 1 |
| 7500-8000 | | | | | | | 1 | | | | 1 |
| Total | 3 | 5 | 6 | 5 | 6 | 9 | 10 | 6 | 4 | 1 | 55 |

*The correlation of eight-months milk production at a given age with the eight-months milk production at any other given age*

For a firm foundation of our practical agriculture, particularly dairying, knowledge of the inter-relationships of the workings of the mammary functions at one age in comparison with its precision of action at another age can scarcely be too exact. The existing practice is, as already pointed out, largely empirical in its nature, often leading to questionable results. The reflection of the questionable nature of these practices is seen in the not uncommon practice of dairymen neglecting the records of the first lactation as a measure of the cow's possibilities for future production.

TABLE 34

*Correlation surface for amount of eight-months milk production at six years old and amount of eight-months milk production at seven years old for pure-bred Jersey cows.*

| 7 years old \ 6 years old | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | 9000-9500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | | | 1 | 1 | | | | | | | | | | | 2 |
| 2500-3000 | 1 | | | | | | | | | | | | | | 1 |
| 3000-3500 | | 1 | 2 | 2 | | | | | | | | | | | 5 |
| 3500-4000 | | 2 | 4 | 2 | 1 | 1 | | 2 | | | | | | | 12 |
| 4000-4500 | | | 1 | 4 | 2 | 3 | | 1 | 1 | | | | | | 12 |
| 4500-5000 | | | 3 | 2 | 6 | 5 | 2 | | | | | | | | 18 |
| 5000-5500 | 1 | | 1 | 4 | 1 | 5 | 3 | 2 | 3 | | | 2 | | | 22 |
| 5500-6000 | | | 1 | 1 | 1 | 2 | 3 | 4 | 1 | 1 | | | | | 14 |
| 6000-6500 | | | | 1 | | 3 | 2 | 7 | | 1 | 1 | | | | 15 |
| 6500-7000 | | | | | 1 | 1 | 3 | 3 | | 2 | 1 | | | | 11 |
| 7000-7500 | | | | | 1 | | 1 | 1 | 1 | 1 | 1 | | | | 6 |
| 7500-8000 | | | | | | | 1 | | | | | 1 | | | 2 |
| 8000-8500 | | | | | | | | 1 | | | 1 | | | 1 | 3 |
| 8500-9000 | | | | | | | | | | 1 | | | | | 1 |
| Total | 2 | 3 | 13 | 17 | 13 | 20 | 15 | 21 | 6 | 6 | 4 | 3 | 0 | 1 | 124 |

The correlations between the milk production of various lactations with one another have material importance as well as theoretical interest for these problems. If the correlation is high it is evident from the practical side that the culling of the herd through the use of dependable criteria will result in the increase of profits to its owners. From the biological side, a high correlation means that the animals composing the herd are innately differentiated (presumably due to their inherited complex) in their mammary capacities.

TABLE 35

*Correlation surface for amount of eight-months milk production at six years old and amount of eight-months milk production at eight and nine years old for pure-bred Jersey cows.*

| 6 years old \ 8 and 9 years old | 2000-2500 | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | 9000-9500 | 9500-1000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2500-3000 | | 1 | 1 | | | | 1 | 1 | | | | | | | | | 4 |
| 3000-3500 | | 1 | 2 | 2 | | | | | | | | | | | | | 5 |
| 3500-4000 | | | 1 | 2 | 4 | 3 | 1 | | | | | | | | | | 11 |
| 4000-4500 | 1 | | 2 | 2 | 1 | | 2 | 1 | 3 | 1 | 1 | | | | | | 14 |
| 4500-5000 | | 2 | 4 | 1 | 3 | 6 | 6 | 1 | 3 | 2 | | | | | | | 28 |
| 5000-5500 | | 1 | 1 | 2 | 1 | 4 | 4 | | 3 | 2 | 1 | 1 | | | | | 20 |
| 5500-6000 | | | | | 3 | 2 | 5 | 3 | 5 | 1 | 1 | | | | | | 20 |
| 6000-6500 | 1 | | | | 3 | 2 | 6 | 4 | | 3 | 1 | | | | | | 20 |
| 6500-7000 | | | | | | 1 | 3 | 1 | | 3 | | | | | | 1 | 9 |
| 7000-7500 | | | | | | 1 | 2 | 2 | 4 | 1 | | | 1 | | | | 11 |
| 7500-8000 | | | | | | | | | | 1 | 1 | | | | | | 2 |
| 8000-8500 | | | | | | | 1 | 1 | | 1 | 1 | | | | | | 4 |
| Total | 2 | 5 | 11 | 9 | 15 | 19 | 31 | 14 | 18 | 15 | 6 | 1 | 1 | 0 | 0 | 1 | 148 |

The determination of the correlations for these data is of especial interest, for, as previously shown in the earlier part of this paper, the data are of exceptional value in that they are on a pure-bred Jersey herd kept intact for many years; the lactation records for several lactations are recorded on a number of the animals; and the herd has been subject to no detectable culling based on the production of a given lactation. From these data there have been extracted lactation records to the number of 3178 pairs having a full eight-months lactation free from any disease or sickness or other trouble known to influence the records. These records have been formed into twenty-eight correlation tables the most of which are of considerable size.

After careful consideration it was decided that since these tables have much of scientific and practical value to the practice of dairy husbandry they had better be printed *in toto*. These tables are reproduced in the text tables numbers 9 to 40.

The means, standard deviations and coefficients of variation for these correlation tables have been presented in tables 11, 20 and 25. Table 32 gives the correlations and their probable errors for all ages at which the lactation records were divided. The vertical columns give the correlations of the milk production at the age heading the column with the

TABLE 36

*Correlation surface for amount of eight-months milk production at six years old and amount of eight-months milk production at ten years and older for pure-bred Jersey cows.*

| 10-and-above years old \ 6 years old | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | | | 1 | | | | | | | | 1 |
| 2500-3500 | | | | | | 1 | | | | | 1 |
| 3000-3500 | 1 | 1 | | 1 | | 1 | | | | | 4 |
| 3500-4000 | | | 2 | | | 1 | | 2 | | | 5 |
| 4000-4500 | | | 1 | | 2 | | 3 | 1 | | 1 | 8 |
| 4500-5000 | | | 2 | •1 | 4 | 2 | 2 | 3 | | 1 | 15 |
| 5000-5500 | | 1 | 1 | | 2 | 1 | 3 | 5 | 1 | | 14 |
| 5500-6000 | | | | | 4 | | 1 | 2 | | | 7 |
| 6000-6500 | | | | 1 | | | | 3 | 1 | | 5 |
| 6500-7000 | | | | | | | | | | 3 | 3 |
| 7000-7500 | | | | | | | | 1 | | | 1 |
| Total | 1 | 2 | 7 | 3 | 12 | 6 | 9 | 17 | 2 | 5 | 64 |

TABLE 37

*Correlation surface for amount of eight-months milk production at seven years old and amount of eight-months milk production at eight and nine years old for pure-bred Jersey cows.*

| 7 years old \ 8 and 9 years old | 2000-2500 | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | 7500-8000 | 8000-8500 | 8500-9000 | 9000-9500 | 9500-10000 | 10000-10500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2500-3000 | | 1 | 1 | | | | | | | | | | | | | | | 2 |
| 3000-3500 | 1 | 1 | 1 | 2 | 2 | | 1 | | | | | | | | | | | 8 |
| 3500-4000 | | | 3 | 3 | 5 | 3 | 3 | | | | | | | | | | | 17 |
| 4000-4500 | 1 | 1 | | 3 | 1 | 2 | 4 | 1 | | 1 | | | | | | | | 14 |
| 4500-5000 | | 1 | 3 | 5 | 2 | 6 | 5 | 2 | 2 | 1 | | | | | | | | 27 |
| 5000-5500 | | 1 | | 2 | 3 | 2 | 5 | 3 | 3 | 2 | 2 | | | | | | | 23 |
| 5500-6000 | | | | 1 | 1 | 2 | 6 | 1 | 3 | 1 | 3 | | | | | | | 18 |
| 6000-6500 | 1 | | | | 4 | 4 | 2 | 1 | 3 | 2 | | | | | | | | 17 |
| 6500-7000 | | | | | 2 | 1 | 3 | 4 | 2 | 2 | 1 | | | | | | | 15 |
| 7000-7500 | | | | | | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | | | 1 | | 8 |
| 7500-8000 | | | | | | | | | | 1 | | | | | | | 1 | 2 |
| Total | 3 | 5 | 8 | 16 | 20 | 20 | 30 | 13 | 14 | 11 | 7 | 1 | 1 | 0 | 0 | 1 | 1 | 151 |

milk production at the ages indicated at the left-hand margin of the table.

As will be noted the correlations necessary to give the complete set of correlations for any given age are repeated, e.g., the correlation of milk production at 2 years with that at 3 years is +0.5764±.0332 and appears in the 2-year column. The correlation of the 3-years milk production with that of 2 years will, of course, be the same (0.5764±.0332) and is repeated in the three-year column. In this manner a complete picture of the relationship of the lactations of the 2-year groups with the other lactations of the other groups is given in the column.

TABLE 38

*Coefficients of correlation of milk production of a given age with the milk production of another given age.*

| Age | 2-3 years | 3-4 years | 4-5 years | 5-6 years |
|---|---|---|---|---|
| 2 to 3 | | +0.5764 ± .0332 | +0.5426 ± .0361 | +0.5373 ± .0406 |
| 3 to 4 | +0.5764 ± .0332 | | +0.6206 ± .0335 | +0.5479 ± .0395 |
| 4 to 5 | +0.5426 ± .0361 | +0.6206 ± .0335 | | +0.5541 ± .0391 |
| 5 to 6 | +0.5373 ± .0406 | +0.5479 ± .0395 | +0.5541 ± .0391 | |
| 6 to 7 | +0.5500 ± .0426 | +0.5305 ± .0452 | +0.5624 ± .0421 | +0.7306 ± .0284 |
| 7 to 8 | +0.5815 ± .0468 | +0.5394 ± .0483 | +0.6328 ± .0380 | +0.5667 ± .0403 |
| 8 to 10 | +0.4938 ± .0488 | +0.5376 ± .0465 | +0.4154 ± .0503 | +0.5405 ± .0397 |
| 10 and older | +0.5603 ± .0732 | +0.6336 ± .0925 | +0.2144 ± .0919 | +0.5371 ± .0697 |

TABLE 38 (continued)

*Coefficients of correlation of milk production of a given age with the milk production of another given age.*

| Age | 6-7 years | 7-8 years | 8-10 years | 10 years and older |
|---|---|---|---|---|
| 2 to 3 | +0.5500 ± .0426 | +0.5815 ± .0468 | +0.4938 ± .0488 | +0.5603 ± .0732 |
| 3 to 4 | +0.5305 ± .0452 | +0.5394 ± .0483 | +0.5376 ± .0165 | +0.6336 ± .0925 |
| 4 to 5 | +0.5624 ± .0421 | +0.6328 ± .0380 | +0.4154 ± .0503 | +0.2144 ± .0919 |
| 5 to 6 | +0.7306 ± .0284 | +0.5667 ± .0403 | +0.5405 ± .0397 | +0.5371 ± .0697 |
| 6 to 7 | | +0.6515 ± .0349 | +0.4800 ± .0427 | +0.4578 ± .0666 |
| 7 to 8 | +0.6515 ± .0349 | | +0.5750 ± .0367 | +0.3036 ± .0712 |
| 8 to 10 | +0.4800 ± .0427 | +0.5750 ± .0367 | | +0.5113 ± .0448 |
| 10 and older | +0.4578 ± .0666 | +0.3036 ± .0712 | +0.5113 ± .0448 | |

The order of magnitude of these correlations is from +0.7306 for the correlation of 8-months milk productions during the ages 5 to 6 and 6 to 7 years, and +0.2144 for the correlation of the productions during the ages 4 to 5 and 10 years and older. Such correlations indicate that the milk production of one lactation may be predicted with relatively little inaccuracy from the milk production of another lactation. The graphs showing these correlations for each year are seen in figure 9.

The arrangement of this figure is similar to that of figure 6. The magnitudes of the correlations are represented as ordinates. The ages of the cows whose productions are correlated with those of the given age are represented as abscissae. The curves progressing from top to bottom of the figure represent the correlations of the 8-months milk productions at the ages two, three, four, five, six, seven, eight and nine, and over ten years with the eight-months productions occurring at the other ages shown on the lower margin of the figure.

The graph for the correlation coefficients of the milk production at two years with the milk production of the subsequent lactations of the same cows shows little deviation from a straight line. The values of these correlations range from $+0.4938\pm.0488$ to $+0.5815\pm.0468$. The values for the three-year correlations with the other years range somewhat higher, $+0.5305\pm.0452$ to $+0.6336\pm.0925$. These correlations would be quite accurately described by a linear function. The values of the correlation of the four-year-olds' production with those of other years range from $+0.2144\pm.0919$ to $+0.6328\pm.0380$. On the whole these values are slightly lower than are those for other years. The values for the five-year-olds range from $+0.5371\pm.0697$ to $+0.7306\pm.0284$. These values are the highest in their range of any of the ages. The correlations for the six-year productions with those of other ages range from $0.4578\pm.0666$ to $+0.7306\pm.0284$. The correlations for the seven-year productions range from $0.3036\pm.0712$ to $+0.6515\pm.0349$. The correlations for the 8-and-9-year period range from $+0.4154\pm.0503$ to $+0.5750\pm.0367$ and the correlations for the productions at 10 years and older with those of the younger years range from $+0.2144\pm.0919$ to $+0.6336\pm.0925$. From this brief resumé of the tabled results it is seen that all of the results have the plus sign and have a rather large value for data of this kind. The values of the coefficients are in general higher for the younger ages than they are for the older ages. This is a fortunate circumstance from a practical standpoint for the breeder is more desirous of selecting the animals to remain in the herd from their two-year records than he is to select his animals at ten years old. The values of the correlations are fortunately such that a gain in accuracy results by predicting from the two-year-olds as over predictions at later ages.

From the practical side of culling the poor milkers out of the herd these results are highly satisfactory. The data are equally interesting when considered in their biological aspects. The correlations show that the cows composing the herd are innately differentiated in their milk-

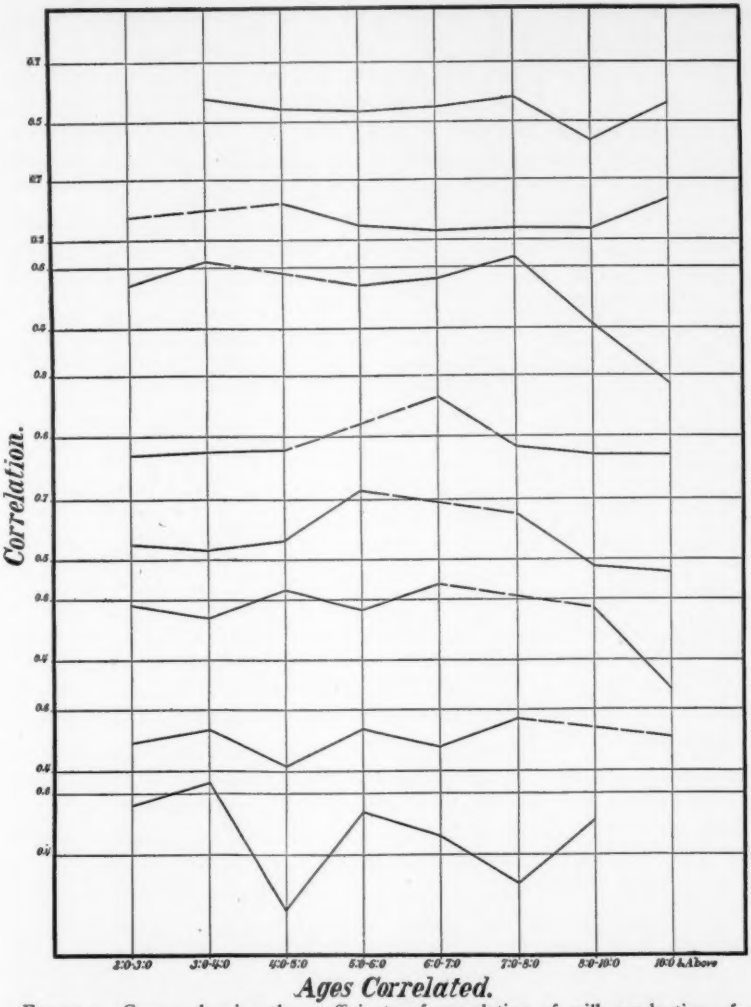


FIGURE 9.—Curves showing the coefficients of correlation of milk production of a given age and the milk production occurring at any other given age. The ordinates are the values of the correlation coefficients. The abscissae are the ages at which the lactation record compared with the record at the given age, was made. Thus the top curve of the figure shows the correlations of records made at two years old with the records made at subsequent ages. From this curve the correlation between two-years milk production and three-years milk production is found on the three-year line of the two-year curve (top curve of figure) to be 0.5764. The correlation of the two-year and four-year record is found on the four-year line where the two-year line crosses it (top curve of figure) to be 0.5426, etc. The dotted lines serve to connect the correlations immediately preceding and following the age for which the line is drawn.

TABLE 39

*Correlation surface for amount of eight-months milk production at seven years old and amount of eight-months milk production at ten years and older for pure-bred Jersey cows.*

7 years old

| 10-and-above years old | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | | | | | 1 | | | | | | 1 |
| 2500-3000 | | | | 1 | | | 1 | | | | 2 |
| 3000-3500 | 1 | | 1 | | 1 | 3 | | 1 | | | 7 |
| 3500-4000 | | 1 | | 1 | 1 | 2 | | | | | 5 |
| 4000-4500 | | | 1 | 1 | 2 | 2 | 4 | 1 | | | 11 |
| 4500-5000 | | 1 | 2 | 4 | 3 | 1 | 3 | 1 | 1 | 1 | 17 |
| 5000-5500 | | 1 | 4 | | 2 | | 3 | 2 | 1 | 1 | 14 |
| 5500-6000 | | | | | 1 | | 2 | 1 | 1 | 2 | 7 |
| 6000-6500 | | | | | | 1 | 4 | | | | 5 |
| 6500-7000 | | | | | | 1 | 1 | | | | 2 |
| 7000-7500 | | | | 1 | | | | 1 | | | 2 |
| 7500-8000 | | | | | | | | | 1 | | 1 |
| Total | 1 | 3 | 8 | 8 | 11 | 10 | 18 | 7 | 4 | 4 | 74 |

TABLE 40

*Correlation surface for amount of eight-months milk production at eight and nine years old and amount of eight-months milk production at ten years old and older for pure-bred Jersey cows.*

8 and 9 years old

| 10-and-above years old | 2500-3000 | 3000-3500 | 3500-4000 | 4000-4500 | 4500-5000 | 5000-5500 | 5500-6000 | 6000-6500 | 6500-7000 | 7000-7500 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | | 1 | | 1 | | | | | | | 2 |
| 2500-3000 | | | 1 | | 1 | 1 | | | | | 3 |
| 3000-3500 | 2 | 2 | 3 | 2 | | 1 | | 1 | | | 11 |
| 3500-4000 | | | 2 | 2 | 2 | | | | 2 | | 8 |
| 4000-4500 | | 1 | 3 | 2 | 3 | 5 | | 2 | 1 | 1 | 18 |
| 4500-5000 | 1 | 1 | 5 | 2 | 4 | 10 | 2 | | 2 | | 27 |
| 5000-5500 | | | 2 | 3 | 2 | 6 | | 5 | 4 | 1 | 23 |
| 5500-6000 | | | | 1 | | 3 | 2 | 2 | 5 | | 13 |
| 6000-6500 | | | | | | 1 | | 1 | 1 | 2 | 5 |
| 6500-7000 | | | | | | 5 | 1 | 2 | | 1 | 9 |
| 7000-7500 | | | | | | 1 | | 1 | 1 | | 3 |
| 7500-8000 | | | | | | | 1 | | 1 | | 2 |
| Total | 3 | 5 | 16 | 13 | 12 | 33 | 6 | 14 | 17 | 5 | 124 |

producing abilities. The plane of producton once established the cow tends to maintain this relative plane from lactation to lactation. The values of the correlations indicate clearly that there is a fairly accurately working mechanism behind this function.

From this point of view it is of a good deal of interest to compare the only other statistics available for cattle, with those derived here. GAVIN (1913) using his measure of the lactation as the "revised maximum" found the correlation between the milk productions of the various lactations and that of their maximum "revised maximum" GAVIN (1912). Table 41 is a copy of GAVIN's table showing these correlations.

TABLE 41

| Lactation | $r$ with maximum "revised maximum" | Probable error |
|---|---|---|
| First | + .394 | ± 0.031 |
| Second | + .452 | ± 0.030 |
| Third | + .506 | ± 0.028 |
| Fourth | + .605 | ± 0.024 |
| Fifth | + .762 | ± 0.016 |

This table shows in general a lower value for the correlations measuring the consistency of milking performance from lactation to lactation than is shown by our data. This may in part be due to the fact that GAVIN's material was somewhat heterogeneous, including data from British Holsteins and Shorthorns. In all events, the correlations confirm our general conclusions that milk production of one lactation is quite closely correlated with that of the other lactations. This reasoning transferred to the individuals of the race of dairy cattle, appears to prove beyond any shade of doubt that the individuals of the race are innately differentiated as regards the capacity for milk production.

Of the quantitative data on other species of practical interest perhaps the most complete is that of HARRIS and BLAKESLEE (1918) on the White Leghorn. In this work they determined the correlations between the monthly egg production and the other-eleven-months production of the same bird. The correlations for these monthly ovulations with the other-eleven-months ovulation take values ranging from $+0.240 \pm .033$ to $+0.573 \pm .023$. The range is there quite similar to those obtained in this although lower in value. The knowledge of these sets of constants gives criteria for the fairly accurate prediction of the records that may be expected at a subsequent date in the life of these two species of extreme economic importance.

THE REGRESSION OF THE MILK PRODUCTIONS OF THE DIFFERENT LACTATIONS ON EACH OTHER

The constants necessary to determine the approach of the regression to linearity are given in table 42. The values of the correlation coefficients have been repeated for greater ease in drawing conclusions from the values of the correlation ratios.

In this table the values of the correlation ratios range from 0.4382 to 0.8189. The conclusions drawn from a study of the correlation coefficients is thus confirmed by these correlation ratios.

As is generally well recognized, the coefficients of correlation depend for their accuracy on the regression lines being closely described by a linear function. The values of the correlation ratio on the other hand do not depend on this fitting of linear functions to the rough regression lines but do give a measure of the association from the regression line itself. If this rough regression is linear the two constants should agree within the limits of their probable errors. In table 42 columns $\eta - r$ and $\eta^2 - r^2$ give constants to measure this agreement. The last column gives the multiple number of times $\eta^2 - r^2$ is to the probable error. This column gives us in a form easily appreciated the measure of what significance can be attached to these constants. The values range from 0.33 to 4.46, from an insignificant deviation to one probably significant. Of the 28 values only six are less than 2 times their probable error. The average of the 28 constants shows that the mean deviation is 2.42 times the probable error. On the face of this it would seem that there is a slight deviation of the regression lines from the linear. This deviation may be due to the duration of life covered by the age units within which the lactation records were correlated. These units were in general of one year in length. During this time, as was shown earlier in this paper, there is a non-linear rise in milk production. One year appears to be of sufficient length of time to have produced this effect in the milk yield. To this effect the appearance of a regression differing slightly from the linear may be attributed. It would appear that should a shorter unit of time be chosen, the value of the correlation coefficients would agree more closely with those of the correlation ratios.

This reasoning, while apparently probable, does not prove true, as a later section of the paper dealing with regressions over five lactations shows. This slight lack of linearity must therefore be considered due either to chance or to some obscure causes. In any case it will not influence the results materially where the correlations are used as constants for calculation.

TABLE 42

*Analytical constants for intra-individual variation of cow's milk from lactation to lactation.*

| Character | $r$ | $\eta$ | $\eta - r$ | $\eta^2 - r^2$ | $\frac{\eta^2 - r^2}{E_{\eta^2 - r^2}}$ |
|---|---|---|---|---|---|
| 2 years to 3 years | +0.5764 ± .0332 | +0.6275 ± .0301 | 0.0512 ± .0448 | 0.0615 ± .0239 | 2.58 |
| " " 4 " | .5425 ± .0360 | .5922 ± .0332 | .0496 ± .0490 | .0563 ± .0236 | 2.39 |
| " " 5 " | .5373 ± .0406 | .6348 ± .0340 | .0976 ± .0530 | .1143 ± .0363 | 3.15 |
| " " 6 " | .5500 ± .0426 | .6206 ± .0375 | .0706 ± .0568 | .0826 ± .0336 | 2.46 |
| " " 7 " | .5815 ± .0468 | .6607 ± .0398 | .0792 ± .0614 | .0984 ± .0421 | 2.34 |
| " "8 and 9" | .4938 ± .0488 | .6033 ± .0411 | .1095 ± .0638 | .1201 ± .0420 | 2.86 |
| " " 10 and older | .5603 ± .0732 | .7081 ± .0532 | .1478 ± .0905 | .1875 ± .0832 | 2.25 |
| 3 years to 4 years | .6206 ± .0335 | .7592 ± .0231 | .1386 ± .0407 | .1912 ± .0429 | 4.46 |
| " " 5 " | .5479 ± .0395 | .6648 ± .0315 | .1169 ± .0505 | .1418 ± .0393 | 3.60 |
| " " 6 " | .5305 ± .0452 | .6129 ± .0393 | .0823 ± .0599 | .0942 ± .0368 | 2.56 |
| " " 7 " | .5394 ± .0483 | .6381 ± .0404 | .0987 ± .0630 | .1162 ± .0437 | 2.66 |
| " "8 and 9" | .5376 ± .0465 | .6083 ± .0413 | .0707 ± .0622 | .0810 ± .0358 | 2.27 |
| " " 10 and older | .6336 ± .0925 | .8189 ± .0509 | .1853 ± .1056 | .2691 ± .1409 | 1.91 |
| 4 years to 5 years | .5541 ± .0391 | .5661 ± .0383 | .0120 ± .0547 | .0134 ± .0411 | .33 |
| 4 " 6 " | .5624 ± .0421 | .6186 ± .0380 | .0562 ± .0567 | .0664 ± .0306 | 2.17 |
| 4 " 7 " | .6328 ± .0380 | .7163 ± .0309 | .0835 ± .0490 | .1127 ± .0401 | 2.81 |
| 4 "8 and 9" | .4154 ± .0503 | .5359 ± .0433 | .1205 ± .0664 | .1146 ± .0387 | 2.96 |
| " " 10 and older | .2144 ± .0919 | .5353 ± .0588 | .3208 ± .1148 | .2406 ± .0824 | 2.92 |
| 5 years to 6 years | .7306 ± .0284 | .7552 ± .0263 | .0246 ± .0387 | .0366 ± .0229 | 1.59 |
| " " 7 " | .5667 ± .0403 | .6638 ± .0332 | .0971 ± .0522 | .1195 ± .0385 | 3.10 |
| " "8 and 9" | .5405 ± .0397 | .6617 ± .0315 | .1212 ± .0507 | .1457 ± .0395 | 3.69 |
| " " 10 and older | .5371 ± .0647 | .6816 ± .0486 | .1445 ± .0800 | .1761 ± .0693 | 2.54 |
| 6 years to 7 years | .6515 ± .0349 | .6712 ± .0333 | .0198 ± .0482 | .0261 ± .0193 | 1.35 |
| " "8 and 9" | .4800 ± .0427 | .5385 ± .0393 | .0585 ± .0580 | .0596 ± .0262 | 2.27 |
| " " 10 and older | .4578 ± .0666 | .5722 ± .0567 | .1145 ± .0875 | .1178 ± .0544 | 2.17 |
| 7 years to 8 and 9 years | .5750 ± .0367 | .5827 ± .0352 | .0077 ± .0515 | .0089 ± .0103 | .86 |
| " " 10 years and older | .3036 ± .0712 | .4382 ± .0634 | .1346 ± .0953 | .0998 ± .0470 | 2.12 |
| 8 and 9 years to 10 years and older | .5113 ± .0448 | .5356 ± .0432 | .0243 ± .0622 | .0253 ± .0100 | 1.33 |

From these correlation coefficients in tables 41 and 42 it is possible to form the straight-line prediction of the milk yield of any age from the yield of any other age. As emphasized repeatedly in the various sections of this paper dealing with the separate subjects, the predictions may be criticised on the following grounds: that the mean milk yield rises with age in a line described by a logarithmic function; that the standard deviation of this milk yield rises in line described by a cubic parabola; and that the values of the correlation coefficients differ from the values of the correlation ratios by 2.42 times the probable error of $\eta^2 - r^2$. Such criticisms are recognized and admitted at once. It is believed that even admitting these there are a number of important points which may be elucidated by these equations.

The general equation for these regressions is given by

$$Y = (\text{Mean}_Y - r_{Yy}\frac{\sigma_Y}{\sigma_y}\text{Mean}_y) + r_{Yy}\frac{\sigma_Y}{\sigma_y}y$$

where $y$ = 8-months milk yield in a given year and $Y$ the expected milk yield for the year desired. The results of the substitution of the values of tables 11 to 42 in this equation are given in table 43.

As the milk production is given in pounds the second term of each of these equations gives the gain in expected milk yield for the given age, if one pound increase in actual production is made during the test. The calculation of an expected yield is, therefore, a simple matter of direct substitution.

Before discussing the relative practical and theoretical merits of these equations for the study of milk records it may be well to take up the equations individually. The coefficients of the $y$'s (actual yields) represent the reliance that may be put on these actual yields for subsequent productions. The information desired by those who use these coefficients for actual records may be divided into two heads: (1) At what age should the cow make her record to give the best index of her potential producing abilities? (2) To what age should the records, made at different periods in the life of the cow, be corrected so that the maximum reliance may be placed on the corrected record?

The first of these questions entails a study of the coefficients of the $y$'s for the ages at which the record was made. The data for this are given in table 44. The equations in this table are of no value save for this comparison, for if any record is to be corrected the equations in table 43 should be used.

TABLE 43

*Regression equations of the milk yield for any age from that of any lactation record at another age.*

| Age at which milk yield was made | Age at which expected milk yield is desired | | | |
|---|---|---|---|---|
| | 2 years to 3 years | 3 years to 4 years | 4 years to 5 years | 5 years to 6 years |
| | Regression equation | Regression equation | Regression equation | Regression equation |
| 2 years to 3 years $y_2$ | | $Y = 1515.5 + .7922y_2$ | $Y = 1447.4 + .8591y_2$ | $Y = 1795.7 + .8968y_2$ |
| 3 years to 4 years $y_3$ | $Y = 2130.0 + .4194y_3$ | | $Y = 2013.7 + .6500y_3$ | $Y = 2082.5 + .6882y_3$ |
| 4 years to 5 years $y_4$ | $Y = 2391.2 + .3427y_4$ | $Y = 1656.2 + .5935y_4$ | | $Y = 2007.2 + .6325y_4$ |
| 5 years to 6 years $y_5$ | $Y = 2394.4 + .3219y_5$ | $Y = 2408.3 + .4362y_5$ | $Y = 2513.3 + .4855y_5$ | |
| 6 years to 7 years $y_6$ | $Y = 2456.2 + .3018y_6$ | $Y = 2346.6 + .4330y_6$ | $Y = 3092.2 + .3652y_6$ | $Y = 1624.4 + .6708y_6$ |
| 7 years to 8 years $y_7$ | $Y = 1995.3 + .3955y_7$ | $Y = 2252.6 + .4790y_7$ | $Y = 2345.0 + .5149y_7$ | $Y = 2507.8 + .5086y_7$ |
| 8 years to 10 years $y_8$ | $Y = 2570.8 + .2927y_8$ | $Y = 2437.6 + .4433y_8$ | $Y = 3367.9 + .3298y_8$ | $Y = 2715.2 + .4959y_8$ |
| 10 years and above $y_{10}$ | $Y = 2633.1 + .3105y_{10}$ | $Y = 868.8 + .8766y_{10}$ | $Y = 3952.6 + .2190y_{10}$ | $Y = 2905.2 + .5265y_{10}$ |

TABLE 43 (continued)

*Regression equations of the milk yield for any age from that of any lactation record at another age.*

| Age at which milk yield was made | Age at which expected milk yield is desired | | | |
|---|---|---|---|---|
| | 6 years to 7 years | 7 years to 8 years | 8 years to 10 years | 10 years and above |
| | Regression equation | Regression equation | Regression equation | Regression equation |
| 2 years to 3 years $y_2$ | $Y = 1551.7 + 1.0023y_2$ | $Y = 1910.8 + .8549y_2$ | $Y = 1710.8 + .8329y_2$ | $Y = 717.0 + 1.010y_2$ |
| 3 years to 4 years $y_3$ | $Y = 2578.2 + .6500y_3$ | $Y = 2502.2 + .6075y_3$ | $Y = 2036.3 + .6519y_3$ | $Y = 2539.6 + .4580y_3$ |
| 4 years to 5 years $y_4$ | $Y = 1158.8 + .8662y_4$ | $Y = 1435.1 + .7778y_4$ | $Y = 2500.7 + .5233y_4$ | $Y = 3711.3 + .2100y_4$ |
| 5 years to 6 years $y_5$ | $Y = 1332.7 + .7958y_5$ | $Y = 2165.0 + .6314y_5$ | $Y = 2087.7 + .5890y_5$ | $Y = 1871.7 + .5480y_5$ |
| 6 years to 7 years $y_6$ | | $Y = 1779.2 + .6585y_6$ | $Y = 2493.0 + .5019y_6$ | $Y = 2681.7 + .4147y_6$ |
| 7 years to 8 years $y_7$ | $Y = 1960.8 + .6445y_7$ | | $Y = 1573.3 + .6720y_7$ | $Y = 3205.1 + .3129y_7$ |
| 8 years to 10 years $y_8$ | $Y = 2989.5 + .4591y_8$ | $Y = 2720.5 + .4920y_8$ | | |
| 10 years and above $y_{10}$ | $Y = 2899.8 + .5053y_{10}$ | $Y = 3772.8 + .2946y_{10}$ | $Y = 2660.1 + .5150y_{10}$ | $Y = 2271.5 + .5075y_8$ |

TABLE 44

*Average regression equations of milk records at the same age for the expected records made throughout the life of the cow. (Summarized from table 43.)*

| Age at which milk record was made | Regression equation |
|---|---|
| 2 years to 3 years | $Y = 1521.3 + .8927y_2$ |
| 3 " to 4 " | $Y = 2268.9 + .5893y_3$ |
| 4 " to 5 " | $Y = 2122.9 + .5637y_4$ |
| 5 " to 6 " | $Y = 2110.4 + .5440y_5$ |
| 6 " to 7 " | $Y = 2353.3 + .4780y_6$ |
| 7 " to 8 " | $Y = 2262.8 + .5039y_7$ |
| 8 " to 10 " | $Y = 2724.7 + .4315y_8$ |
| 10 years and over | $Y = 2813.2 + .4639y_{10}$ |

These data in table 44 show the average values of the regression equations for each age. The coefficients of the *y*'s are the largest at the early years of the cow's life. While quite irregular the values tend to decline as the age when the lactation is made increases. Practically considered this manner of decline is very fortunate. The first lactation being the one most accurately measuring the expectation of the cow in subsequent years enables the farmer or dairymen to determine with greatest certainty from this lactation what the cow is most likely to produce. On this basis the herd may be culled of the poor producers after the first lactation in full knowledge that they would always remain relatively low milkers throughout their life time. Theoretically considered the trend of this decline is of equal interest. Most published records on all breeds of cattle have the greatest number of cattle tested when two years old. It is of considerable consequence, therefore to have the records of the two-year-olds a reasonably accurate measure of the cow's milking capacity. It is of further interest to know that these two-year-olds are the most dependable index of this producing ability.

The data in table 45 summarize the information necessary to deal with the second question. As for table 44 the equations are of no value save for the comparison in hand. If any record is to be corrected the equations of table 43 should be used.

This table shows that the highest values of the coefficients of the *y*'s occurs for the ages 6 years to 7 years. On each side of these ages the values decline toward both the lower and higher years. Practically considered this maximum of the curve shows that the relative potentialities of the cows within the herd is most accurately determined by correcting the records of these animals to the age basis of 6 years to 7 years. This as determined previously in the paper is near the age when the maximum production of this group of Jerseys may be expected.

TABLE 45

*Average regression equations of expected milk records at a given age for records at other ages throughout the life of the cow. (Summarized from table 43.)*

| Age for expected milk yield | Regression equation |
|---|---|
| 2 years to 3 years | $Y = 2367.3 + .3406y_{x-2}$ |
| 3 " to 4 " | $Y = 1926.5 + .5791y_{x-3}$ |
| 4 " to 5 " | $Y = 2676.0 + .4891y_{x-4}$ |
| 5 " to 6 " | $Y = 2234.0 + .6313y_{x-5}$ |
| 6 " to 7 " | $Y = 2067.4 + .7033y_{x-6}$ |
| 7 " to 8 " | $Y = 2326.5 + .6167y_{x-7}$ |
| 8 " to 10 " | $Y = 2151.7 + .6123y_{x-8}$ |
| 10 years and over | $Y = 2428.3 + .4946y_{x-9}$ |

Before turning to other phases of the subject it may be well to discuss the practical and theoretical errors that in some measure vitiate the use of these equations given in table 43. In the practical application the equations will only give values approximately correct. The reason for this is found in an earlier section of the paper where it was shown that milk production is a highly variable character. This variation is sufficient to cause a not inconsiderable difference in the records of certain cows from lactation to lactation. The difference in these records is also expressed in the corrected expected records as calculated from these equations.

The equations are in slight error since they do not take account of the lack of linearity of regression. This difference is such as to make only a very slight error as may be judged by the fact that $\eta^2 - r^2$ is on an average 2.42 times its probable error (page 164).

None of the above errors are very serious drawbacks to the actual use of their equations in practical dairying. The reason for this is simple. The main object for which these equations are of use in a practical sense (the culling the herd of the poor milkers) is little influenced by small errors as the dairyman is not going to select the animals he is going to keep on a difference of one pound. His selections will be as widely separated as possible.

In dealing with milk records from the view-point of inheritance another question should be considered, namely, what makes the regression of the different lactations toward the mean of the general population? Is it an expression of a genotype or is it variation impressed by environment on the genotype in its phenotypic expression? From the general physiological side of milk-production studies the facts all point to the explanation of this regression as principally due to the conditions not

being ideal for the full expression of a cow's potentialities. A few illustrations will make this clear. The work of WING and FOORD (1904) in New York and ECKLES (1912) in Missouri, have shown that meager feeding will reduce the quantity of milk that a cow will produce in a given lactation. WOLL (1902) has reported Danish records to prove that indoor housing decreases milk yield. DOLGICH has shown that working the cows in excess decreases the milk flow. If it is admitted, as it seems it must be that these known variations influence the potential capacities of cows for milk production, it is equally likely that the whole environmental complex in which the cow lives also influences the yield. The studies of PEARL and MINER (1919) indicate these environmental influences amount on an average to as much as one-third of the observed coefficients of variation of the milk of a cow. These environmental influences undoubtedly vary from lactation to lactation and from cow to cow. Such conditions make for regression, for it is only the fortunate coincidence that favors the full expression of the cow's milking capacities. If these considerations are granted as the true state of affairs, inheritance studies of milk production certainly should disregard this regression, as the inclusion of it (as is done by the use of these regression equations) would simply befog the true mechanism if not hide it altogether. Under these circumstances the student of inheritance should use the equation of the mean curve and not the regression equation to count the records of the individual cows, if possible choosing the best record of the series of records as in all probability this represents the fullest expression of the cow's genetic constitution.

### THE CORRELATION OF THE MILK PRODUCTION OF A GIVEN AGE WITH THE TOTAL PRODUCTION OF TWO LACTATIONS

This question and the further extension of it to cover the case of the cow's whole lactation history are of especial interest to the practical dairyman. He is interested primarily in the total yield he may expect from a cow rather than the yield of individual lactation.

Two sets of correlations have been determined to answer this problem; one set on the data as above given where the correlation is between the lactation record of the given year and the lactation records of the given year plus the record of some other year; the second a special set of correlations for the correlation of the summed production for the first five lactations with their component parts.

The first set of correlations may fortunately be calculated without

the formation of the correlation tables from the constants already obtained for tables 11, 20 and 25. The mean and standard deviation of the sum of two components are known when $x = y + z$:

$$\overline{x} = \overline{y} + \overline{z}$$

$$\sigma_x = \sqrt{\sigma_y^2 + \sigma_z^2 + 2r_{yz}\,\sigma_y\,\sigma_z}$$

The product moments are (HARRIS 1917):

$$\Sigma\,(xy) = \Sigma\,(y^2) + \Sigma\,(yz)$$
$$\Sigma\,(xz) = \Sigma\,(z^2) + \Sigma\,(yz)$$

The calculation is then quite simple although tedious. The correlations found by this method are given in table 46.

The correlations are all very large when compared with correlations on most physiological material. They range from $0.7324 \pm .0286$ to $+0.9438 \pm .0116$. Such high values make it appear that the milk production of one lactation is the determining factor for the total milk production of two lactations when the given lactation is one of the components.

This dependence is well worth testing further. For this purpose a series of data including records of five lactations was chosen. Each of the cows whose records were selected began milking in the second year. The five lactations were consecutive and approximately a year apart depending on how long the previous lactations were continued. The lactation records for the five successive lactations were correlated with the total milk production for the five lactations. The correlation coefficients and other constants for these are given in table 47. These constants are calculated from tables 48 to 53.

The high correlation between the record of one lactation and the total production (first five lactation periods) is manifest. The correlations

TABLE 47

| Age when lactation commenced | Mean milk production | Standard deviation for the milk production | Coefficients of variation for the milk production |
|---|---|---|---|
| 2 years to 3 years | 4159.1 ± 57.8 | 803.2 ± 40.8 | 19.31 ± 1.00 |
| 3 years to 4 years | 4840.9 ± 86.1 | 1197.9 ± 60.9 | 24.74 ± 1.35 |
| 4 years to 5 years | 5380.7 ± 78.8 | 1096.2 ± 55.7 | 20.37 ± 1.06 |
| 5 years to 6 years | 5568.2 ± 87.1 | 1211.2 ± 61.6 | 21.75 ± 1.17 |
| 6 years to 7 years | 5681.8 ± 91.4 | 1270.7 ± 64.6 | 22.36 ± 1.17 |
| Total of five lactations | 25613.6 ± 335.9 | 4672.0 ± 237.5 | 18.24 ± .94 |

TABLE 46

*Correlation between the lactation record of a given year and the lactation record of the given year plus the record of some other years.*

| Character* | Correlation | Character | Correlation |
|---|---|---|---|
| 2 and (2 + 3) | +0.8443 ± .0143 | 3 and (2 + 3) | +0.9190 ± .0077 |
| 2 and (2 + 4) | .8133 ± .0173 | 4 and (2 + 4) | .9300 ± .0069 |
| 2 and (2 + 5) | .8030 ± .0202 | 5 and (2 + 5) | .9341 ± .0073 |
| 2 and (2 + 6) | .7961 ± .0224 | 6 and (2 + 6) | .9433 ± .0068 |
| 2 and (2 + 7) | .8404 ± .0208 | 7 and (2 + 7) | .9296 ± .0096 |
| 2 and (2 + 8 and 9) | .7808 ± .0252 | 8 and 9 and (2 + 8 and 9) | .9289 ± .0088 |
| 2 and (2 + 10 and over) | .8026 ± .0379 | 10 and over and (2 + 10 and over) | .9438 ± .0116 |
| 3 and (3 + 4) | .8954 ± .0109 | 4 and (3 + 4) | .9048 ± .0099 |
| 3 and (3 + 5) | .8489 ± .0157 | 5 and (3 + 5) | .9071 ± .0100 |
| 3 and (3 + 6) | .8463 ± .0170 | 6 and (3 + 6) | .9005 ± .0118 |
| 3 and (3 + 7) | .8613 ± .0176 | 7 and (3 + 7) | .8924 ± .0139 |
| 3 and (3 + 8 and 9) | .8503 ± .0182 | 8 and 9 and (3 + 7) | .9009 ± .0123 |
| 3 and (3 + 10 and over) | .9337 ± .0198 | 10 and over and (3 + 10 and over) | .8686 ± .0379 |
| 4 and (4 + 5) | .8643 ± .0143 | 5 and (4 + 5) | .8976 ± .0109 |
| 4 and (4 + 6) | .8559 ± .0165 | 6 and (4 + 6) | .7324 ± .0286 |
| 4 and (4 + 7) | .8816 ± .0141 | 7 and (4 + 7) | .9233 ± .0094 |
| 4 and (4 + 8 and 9) | .7992 ± .0220 | 8 and 9 and (4 + 8 and 9) | .8788 ± .0138 |
| 4 and (4 + 10 and over) | .7845 ± .0371 | 10 and over and (4 + 10 and over) | .7739 ± .0386 |
| 5 and (5 + 6) | .9239 ± .0089 | 6 and (5 + 6) | .9363 ± .0076 |
| 5 and (5 + 7) | .8715 ± .0143 | 7 and (5 + 7) | .8979 ± .0115 |
| 5 and (5 + 8 and 9) | .8661 ± .0140 | 8 and 9 and (5 + 8 and 9) | .8886 ± .0117 |
| 5 and (5 + 10 and over) | .8740 ± .0215 | 10 and over and (5 + 10 and over) | .8793 ± .0207 |
| 6 and (6 + 7) | .9077 ± .0106 | 7 and (6 + 7) | .9097 ± .0104 |
| 6 and (6 + 8 and 9) | .8534 ± .0151 | 8 and 9 and (6 + 8 and 9) | .8669 ± .0138 |
| 6 and (6 + 10 and over) | .8690 ± .0206 | 10 and over and (6 + 10 and over) | .8377 ± .0251 |
| 7 and (7 + 8 and 9) | .8681 ± .0135 | 8 and 9 and (7 + 8 and 9) | .9053 ± .0099 |
| 7 and (7 + 10 and over) | .8006 ± .0281 | 10 and over and (7 + 10 and over) | .8139 ± .0265 |
| 8 and 9 and (8 and 9 + 10 and over) | .8703 ± .0147 | 10 and over and (8 and 9 + 10 and over) | .8682 ± .0149 |

*Under character is recorded first the *age* at which the first lactation record was made. The *and* signifies this lactation record was correlated with the sum of the two lactation records made at the ages indicated in the parenthesis. The *age* at which the first lactation was made is recorded as the term in parenthesis. The *plus* sign signifies that this record was added to the record made at the *age* indicated as the second term of the parenthesis.

TABLE 47 (continued)

| Age when lactation commenced | Correlation of individual lactation records and five-lactations total production | Correlation ratios of individual lactation records and five-lactations total production | Regression equations. Eight-months lactation and five-lactation total production |
|---|---|---|---|
| 2 years to 3 years | +0.7416 ± .0323 | +0.7517 ± .0312 | $Y_T = 7671.9 + 4.3139y_2$ |
| 3 years to 4 years | .8418 ± .0209 | .8856 ± .0155 | $Y_T = 9719.5 + 3.2833y_3$ |
| 4 years to 5 years | .8613 ± .0186 | .8796 ± .0162 | $Y_T = 5861.4 + 3.6710y_4$ |
| 5 years to 6 years | .8250 ± .0230 | .8561 ± .0192 | $Y_T = 7893.5 + 3.1824y_5$ |
| 6 years to 7 years | .8205 ± .0234 | .8468 ± .0203 | $Y_T = 8471.9 + 3.0170y_6$ |
| Total of five lactations | | | |

are so high as to lead to the conclusion that the record of one lactation in a cow's life serves to determine the records for the total production in the cow's life.

The bearing of this conclusion on the mechanism behind the formation of milk is clearly of much significance. The mammary glands may be considered to function because of the interaction of the two variables environment and heredity. Environment may be considered to influence this functioning in two stages; the period during the growth of the cow up to the time she calves and the time after calving when milk is actually secreted. Since this study deals with the records of the same individual cow for successive lactations the inherited complex for her potential milk-producing capacity may be said to be given and constant throughout this work.

The highest possible milk production, or what might be considered the full expression of the hereditary complex, for a given cow may be considered as brought about by ideal environmental conditions for that cow. Taking this definition of the ideal environmental conditions it follows that environmental changes from this condition however slight they may be, are detrimental to the full expression of the mammary gland's possibilities. In a herd like the one with which these data deal no extremely detrimental conditions for any individual cow will exist. The reason for this is clear when it is remembered that the herd has always been kept in the same location under the direction of the same manager thoroughly versed in the feeding and handling of cattle.

Some measure of the influence of environment on the correlation coefficients in the third division into which the mammary functions were divided may be obtained by comparing such coefficients for one lactation period and those covering several lactations. Thus if we correlate

TABLE 48

*Correlation surface for amount of eight-months milk production for the first five lactations in the cow's life and the amount of eight-months milk production at two years old for pure-bred Jersey cows.*

| 2 years old \ Total production for first five lactations (eight-months periods) | 15000-16000 | 16000-17000 | 17000-18000 | 18000-19000 | 19000-20000 | 20000-21000 | 21000-22000 | 22000-23000 | 23000-24000 | 24000-25000 | 25000-26000 | 26000-27000 | 27000-28000 | 28000-29000 | 29000-30000 | 30000-31000 | 31000-32000 | 32000-33000 | 33000-34000 | 34000-35000 | 35000-36000 | 36000-37000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000-2500 | 1 | | | | | | | | | | | | | | | | | | | | | | 1 |
| 2500-3000 | | | 1 | | | 1 | | | | 1 | | | | | | | | | | | | | 3 |
| 3000-3500 | | 1 | 2 | 1 | 1 | 3 | 2 | 2 | 4 | | | 1 | 1 | | | | | | | | | | 18 |
| 3500-4000 | | | | 1 | 2 | | 1 | 3 | 1 | 1 | 3 | | 1 | 1 | | | 1 | | | | | | 15 |
| 4000-4500 | | | | | 1 | | 1 | | 2 | 3 | 1 | 2 | 3 | 2 | 3 | 1 | 1 | | | | | | 20 |
| 4500-5000 | | | | | 1 | | | 1 | 3 | | 2 | 1 | 2 | 2 | 4 | 2 | 1 | 1 | 1 | | | | 21 |
| 5000-5500 | | | | | | | | | | | | | 1 | | 1 | | 1 | 1 | 1 | | | | 5 |
| 5500-6000 | | | | | | | | | | | | | | | 1 | | 1 | | | 1 | | | 3 |
| 6000-6500 | | | | | | | | | | | | | | | | | | | | | 1 | 1 | 2 |
| Total | 1 | 1 | 3 | 2 | 5 | 4 | 4 | 6 | 10 | 5 | 6 | 4 | 8 | 5 | 9 | 3 | 5 | 2 | 2 | 1 | 1 | 1 | 88 |

TABLE 49

*Correlation surface for amount of eight-months milk production for the first five lactations in the cow's life and the amount of eight-months milk production at three years old for pure-bred Jersey cows.*

Total production for first five lactations (eight-months periods)

| 3 years old | 15000-16000 | 16000-17000 | 17000-18000 | 18000-19000 | 19000-20000 | 20000-21000 | 21000-22000 | 22000-23000 | 23000-24000 | 24000-25000 | 25000-26000 | 26000-27000 | 27000-28000 | 28000-29000 | 29000-30000 | 30000-31000 | 31000-32000 | 32000-33000 | 33000-34000 | 34000-35000 | 35000-36000 | 36000-37000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2500-3000 | | | | | | | | | 2 | | | | | | | | | | | | | | 2 |
| 3000-3500 | 1 | 1 | 2 | 2 | 1 | | 1 | 1 | 1 | | | | | | | | | | | | | | 10 |
| 8500-4000 | | | 1 | | 2 | 1 | 3 | 1 | 1 | 1 | 1 | | | | 1 | | | | | | | | 12 |
| 4000-4500 | | | | | 2 | 3 | | 2 | 4 | 1 | 2 | | | | | | | | | | | | 14 |
| 4500-5000 | | | | | | | | 1 | 2 | 2 | 2 | 2 | 4 | 2 | | | | | | | | | 15 |
| 5000-5500 | | | | | | | | 1 | | 1 | 1 | 1 | 2 | 1 | 3 | 1 | 1 | | | | | | 12 |
| 5500-6000 | | | | | | | | | | | | 1 | | 1 | 1 | | 1 | | 1 | | | | 5 |
| 6000-6500 | | | | | | | | | | | | | 2 | 1 | 2 | 1 | 2 | | 1 | | | | 9 |
| 6500-7000 | | | | | | | | | | | | | | | 2 | 1 | | 1 | | | | | 4 |
| 7000-7500 | | | | | | | | | | | | | | | | | | 1 | | 1 | 1 | | 3 |
| 7500-8000 | | | | | | | | | | | | | | | | | 1 | | | | | 1 | 2 |
| Total | 1 | 1 | 3 | 2 | 5 | 4 | 4 | 6 | 10 | 5 | 6 | 4 | 8 | 5 | 9 | 3 | 5 | 2 | 2 | 1 | 1 | 1 | 88 |

TABLE 50

*Correlation surface for amount of eight-months milk production for the first five lactations in the cow's life and the amount of eight-months milk production at four years old for pure-bred Jersey cows.*

| 4 years old \ Total production for first five lactations (eight-month periods) | 15000-16000 | 16000-17000 | 17000-18000 | 18000-19000 | 19000-20000 | 20000-21000 | 21000-22000 | 22000-23000 | 23000-24000 | 24000-25000 | 25000-26000 | 26000-27000 | 27000-28000 | 28000-29000 | 29000-30000 | 30000-31000 | 31000-32000 | 32000-33000 | 33000-34000 | 34000-35000 | 35000-36000 | 36000-37000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 3000-3500 | 1 | 1 | | 1 | | | | | | | | | | | | | | | | | | | 3 |
| 3500-4000 | | | 1 | 1 | 1 | 1 | | | | | | | | | | | | | | | | | 4 |
| 4000-4500 | | | 2 | | 4 | 3 | 1 | | 3 | | 1 | | 1 | | | | | | | | | | 15 |
| 4500-5000 | | | | | | | 1 | 3 | 3 | | | 1 | | | 2 | | | | | | | | 10 |
| 5000-5500 | | | | | | | 2 | 3 | 2 | 5 | 4 | 2 | | | 2 | | 1 | | | | | | 21 |
| 5500-6000 | | | | | | | | | 2 | | 1 | 1 | 5 | 1 | 1 | | | | | | | | 11 |
| 6000-6500 | | | | | | | | | | | | | 1 | 1 | 3 | | | | 1 | | | | 6 |
| 6500-7000 | | | | | | | | | | | | | 1 | 3 | 1 | 2 | 1 | 1 | 1 | 1 | | | 11 |
| 7000-7500 | | | | | | | | | | | | | | | | 1 | 2 | 1 | | | 1 | | 5 |
| 7500-8000 | | | | | | | | | | | | | | | | | 1 | | | | | | 1 |
| 8000-8500 | | | | | | | | | | | | | | | | | | | | | | 1 | 1 |
| Total | 1 | 1 | 3 | 2 | 5 | 4 | 4 | 6 | 10 | 5 | 6 | 4 | 8 | 5 | 9 | 3 | 5 | 2 | 2 | 1 | 1 | 1 | 88 |

TABLE 51

*Correlation surface for amount of eight-months milk production for the first five lactations in the cow's life and the amount of eight-months milk production at five years old for pure-bred Jersey cows.*

| 5 years old \ Total production for first five lactations (eight-months period) | 15000-16000 | 16000-17000 | 17000-18000 | 18000-19000 | 19000-20000 | 20000-21000 | 21000-22000 | 22000-23000 | 23000-24000 | 24000-25000 | 25000-26000 | 26000-27000 | 27000-28000 | 28000-29000 | 29000-30000 | 30000-31000 | 31000-32000 | 32000-33000 | 33000-34000 | 34000-35000 | 35000-36000 | 36000-37000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 3000-3500 | 1 | | 1 | | | | 1 | 1 | | | | | | | | | | | | | | | 4 |
| 3500-4000 | | 1 | 1 | 2 | 2 | 1 | | | | | | | | | | | | | | | | | 7 |
| 4000-4500 | | | 1 | | 1 | | | 1 | 2 | | | | | | | | | | | | | | 5 |
| 4500-5000 | | | | | 1 | 3 | 3 | 3 | 2 | | | | | 1 | | | | | | | | | 13 |
| 5000-5500 | | | | | 1 | | | 1 | 4 | 2 | 2 | | 3 | | 1 | 1 | | | | | | | 15 |
| 5500-6000 | | | | | | | | | 1 | 2 | 1 | 3 | 1 | | 1 | 1 | 1 | | | | | | 11 |
| 6000-6500 | | | | | | | | | 1 | 1 | 2 | | 3 | 2 | 2 | 1 | | 1 | | | | | 13 |
| 6500-7000 | | | | | | | | | | | 1 | | | 1 | 2 | | 2 | | | 1 | | | 7 |
| 7000-7500 | | | | | | | | | | | | 1 | 1 | | 2 | | 1 | 1 | 2 | | 1 | | 9 |
| 7500-8000 | | | | | | | | | | | | | | | 1 | | | | | | | 1 | 2 |
| 8000-8500 | | | | | | | | | | | | | | 1 | | | 1 | | | | | | 2 |
| Total | 1 | 1 | 3 | 2 | 5 | 4 | 4 | 6 | 10 | 5 | 6 | 4 | 8 | 5 | 9 | 3 | 5 | 2 | 2 | 1 | 1 | 1 | 88 |

TABLE 52

*Correlation surface for amount of eight-months milk production for the first five lactations in the cow's life and the amount of eight-months milk production at six years old for pure-bred Jersey cows.*

Total production for first five lactations (eight-months period)

| 6 years old | 15000-16000 | 16000-17000 | 17000-18000 | 18000-19000 | 19000-20000 | 20000-21000 | 21000-22000 | 22000-23000 | 23000-24000 | 24000-25000 | 25000-26000 | 26000-27000 | 27000-28000 | 28000-29000 | 29000-30000 | 30000-31000 | 31000-32000 | 32000-33000 | 33000-34000 | 34000-35000 | 35000-36000 | 36000-37000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 3000-3500 | 1 | | 2 | | | | | | | | | | | | | | | | | | | | 3 |
| 3500-4000 | | 1 | 1 | | 3 | 1 | 1 | | 1 | | | | | | | | | | | | | | 8 |
| 4000-4500 | | | | 1 | 1 | | | 1 | | | | | | | | | | | | | | | 3 |
| 4500-5000 | | | | 1 | 1 | 2 | 2 | 1 | 3 | 2 | | | 1 | | | | | | | | | | 13 |
| 5000-5500 | | | | | | 1 | 1 | 3 | | 1 | 2 | 1 | 1 | 2 | 1 | | 1 | | | | | | 14 |
| 5500-6000 | | | | | | | | 1 | 5 | 1 | 1 | 1 | 1 | | 2 | | | | | | | | 12 |
| 6000-6500 | | | | | | | | | | | 2 | 2 | 3 | 1 | 3 | 1 | 1 | | | | | | 13 |
| 6500-7000 | | | | | | | | | 1 | 1 | 1 | | | 1 | | 1 | | 1 | | | | 1 | 7 |
| 7000-7500 | | | | | | | | | | | | | 1 | 1 | 2 | 1 | 1 | | | | 1 | | 7 |
| 7500-8000 | | | | | | | | | | | | | 1 | | 1 | | 2 | 1 | | 1 | | | 6 |
| 8000-8500 | | | | | | | | | | | | | | | | | | | 1 | | | | 1 |
| 8500-9000 | | | | | | | | | | | | | | | | | | | | | | | 0 |
| 9000-10000 | | | | | | | | | | | | | | | | | | | 1 | | | | 1 |
| Total | 1 | 1 | 3 | 2 | 5 | 4 | 4 | 6 | 10 | 5 | 6 | 4 | 8 | 5 | 9 | 3 | 5 | 2 | 2 | 1 | 1 | 1 | 88 |

TABLE 53

| Lactations correlated | Correlation coefficients | Average correlation coefficients | | Correlation coefficients for given lactation and total of five lactations minus the given lactation | |
|---|---|---|---|---|---|
| 1 and 2 | +0.5991 ± .0461 | 1st lactation | | 1st and | |
| 1 and 3 | .6007 ± .0459 | and 2nd, 3rd, 4th, 5th | 0.5676 ± .0486 | 2 + 3 + 4 + 5 | 0.6475 ± .0418 |
| 1 and 4 | .5671 ± .0488 | 2nd lactation | | 2nd and | |
| 1 and 5 | .5033 ± .0537 | and 1st, 3rd, 4th, 5th | .6284 ± .0430 | 1 + 3 + 4 + 5 | .7352 ± .0331 |
| 2 and 3 | .7785 ± .0284 | 3rd lactation | | 3rd and | |
| 2 and 4 | .5851 ± .0473 | and 1st, 2nd, 4th, 5th | .6445 ± .0416 | 1 + 2 + 4 + 5 | .7768 ± .0285 |
| 2 and 5 | .5509 ± .0501 | 4th lactation | | 4th and | |
| 3 and 4 | .6213 ± .0442 | and 1st, 2nd, 3rd, 5th | .6098 ± .0451 | 1 + 2 + 3 + 5 | .7075 ± .0359 |
| 3 and 5 | .5775 ± .0480 | 5th lactation | | 5th and | |
| 4 and 5 | .6657 ± .0400 | and 1st, 2nd, 3rd, 4th | .5744 ± .0480 | 1 + 2 + 3 + 4 | .6924 ± .0375 |

the milk production of two-year-olds with the total production of the next four lactations and compare these correlations with those for the two-year-olds correlated separately with each of the other lactations we will have a measure of the action of environment in affecting milk production of the cow as against the relatively steady environment over a longer period. The data of table 47 furnish the constants for the necessary calculations of the long-time lactation periods. The calculations for the short time involve the calculation of twelve correlations. These data are shown in table 53.

The correlation coefficients of the given lactation with the total of the first five minus the given lactation are in general about 0.1 higher than the mean correlation coefficient as found by averaging the correlations of the separate lactation with the given one. The consistency of the difference rather than the amount leads to the conclusion that this difference while slight is biologically significant. Such being the case the environment may be roughly said to effect a lowering of the correlation coefficient which on an average amounts to from one-seventh to one-eighth the correlation coefficient of the average environment under which these cows live.

It is impossible to get any accurate means of measuring the relative influence of the environmental conditions of the younger years. From the history of the herd, the standard conditions for all the young stock and the similarity of the feeding, etc., it seems doubtful if such environmental differences as do exist in the calf period are of as great consequence to the subsequent milk production as are such differences in the actual lactation cycle.

These results are in conformity with those of GALTON (1895) for widely different material on the differential action of "nurture and nature" in favoring the much greater influence of nature over nurture in the somatic expression of a character. The intensity with which a given cow maintains a given plane of milk production throughout life indicates a fair degree of precision in the mechanical operation of the inherited factors which appear in large measure to govern the amount of milk produced.

The comparison of the accuracy with which this control mechanism works with that of similar secretions in other species has a good deal of direct bearing on the subject. The only data available are for the egg of the domestic fowl. This egg, like milk, is composed of a number of substances going to make up the whole. It differs from milk in being recorded in number of eggs produced and not in pounds. The eggs are

further produced in clutches, each clutch extending over a short time in the year. These clutches are recurrent and might be considered to parallel the successive lactation cycles. Egg production differs from milk production in a further vital particular. The stimulation of the secretion in an egg depends on the passage down the oviduct of an egg yolk or other foreign body. The amount of egg albumen, etc., secreted depends on the number of egg yolks released from the ovary and not on any innate property of albumen secretion as does the secretion of the parts to form milk. Remembering these differences it is still of a good deal of interest to compare the correlation which may exist between successive periods of egg production and the total number produced in a given period and the correlations for successive periods of milk production and the production for the first five lactations as derived in table 47.

Correlations obtained by HARRIS and BLAKESLEE (1918) for the successive monthly egg productions of White Leghorn pullets with their first annual production, range from $+0.372 \pm .030$ to $0.695 \pm .018$ with an average of 0.556. The correlations of the successive yearly productions and the total of the first five lactations shown in table 47 range from $+0.7416 \pm .0323$ to $0.8613 \pm .0186$. The difference between these correlations is striking. In the proper calculation of this difference it must be remembered that the correlations for egg production is for the twelve-month period where the production for the individual-month correlation contributes only one-twelfth to the total annual egg production while that for the milk production contributes about one-fifth to the total production of the five lactations. The correlation would therefore be expected slightly larger for the milk production. This increased size of the milk correlations over the egg correlations is very small relative to the whole difference, as the confirmatory results of table 38 (page 159) show. The correlations for the milk production of the successive lactations, therefore, represent in concrete terms that a greater reliance may be placed in the milk records of one lactation as measuring the cow's capacity than can be placed in the monthly egg records as measuring the hen's capacity for annual production. Such being the case, if we generalize this conclusion in its ultimate terms, the causative mechanism behind milk production works with greater fineness and precision than does the mechanism for egg production. • Since this mechanism seems in its broadest sense to be of hereditary origin in the two cases, it follows that in the cow this hereditary complex is less influenced in its action by environment than is the action of the material stuffs of the fowl for egg production.

PRACTICAL ASPECT OF THE CORRELATIONS FOR MILK PRODUCTION OF ONE LACTATION RECORD WITH ANOTHER LACTATION RECORD

The constants deduced in table 47 have a good deal of practical value to the dairyman and to the student of farm management. To illustrate, suppose a herd which has 1000 two-year-olds which have just completed their first lactation, is chosen at random. The manager of this herd will wish to know what animals to save for future lactations and the student of farm management desires to know what may be expected for the total production of the animals to enable him to determine the plane to which the herd should be culled for the greatest profit to the owner. The equations derived from table 4 on page 120 allow the determination of the distribution of the cows as to their eight-months yield of milk if the one thousand two-year-old cows are drawn at random from a population similar to that of the Jerseys of these data. The equation for this curve may be repeated for sake of convenience of those who desire to check the results.

$$y = 71.7407 \left(1 - \frac{x^2}{16{,}291{,}354}\right)^{10.648}$$

From the actual eight-months milk production of table 47 the equation to determine the sum of the expected lactation yields of the first five lactations is given by

$$Y_T = 7671.9 + 4.3139 y_2$$

where $Y_T$ is the total expected yield of the five lactations and $y_2$ is the actual yield of the two-year-old cow.

Perhaps one of the easiest ways to table the necessary information for its readiest uses is to have the summation of both the number of cows and their expected total production. This summation to be from both ends of the range of milk produced. The data for such a comparison are given in table 54.

If all the cows in this herd are kept to their sixth lactation the average production for each cow for the five lactations would be 25,070 pounds of milk. Noting the summed number of cows in column four if the 217 poorest producers are culled from the herd the cows left in the herd will produce on an average 26,408 pounds or on an average 5,389 pounds more milk than the culled cows. Again if the dairyman decides to cull out 543 of the thousand animals the production of the 457 remaining will be 28,192 pounds or 5,747 pounds more than the culled cows on the average for the summed productions for the five lactations.

TABLE 54

*Actual milk production of one thousand two-year-old cows and the expected five-lactation yield for any division of that herd or per cow for any division.†*

| Actual milk production | Cows producing given amount | Expected five-lactation yield | Summed number of cows lowest to highest production | Expected summed five-lactation yield for cows in herd lowest to highest production | Summed number of cows highest to lowest production | Expected summed five-lactation yield for cows in herd highest to lowest | Expected production per cow lowest to highest | Expected production per cow highest to lowest |
|---|---|---|---|---|---|---|---|---|
| 1375 to 1625 | 1 | 14143 | 1 | 14,143 | 1000 | 25,069,737 | 14,143 | 25,070* |
| 1625 to 1875 | 2 | 15221 | 3 | 41,355 | 999 | 25,050,000 | 14,822 | 25,076 |
| 1875 to 2125 | 5 | 16300 | 8 | 128,721 | 997 | 25,028,382 | 15,794 | 25,098 |
| 2125 to 2375 | 12 | 17378 | 20 | 335,173 | 992 | 24,941,016 | 16,734 | 25,146 |
| 2375 to 2625 | 23 | 18457 | 43 | 753,397 | 980 | 24,734,564 | 17,649 | 25,240 |
| 2625 to 2875 | 38 | 19535 | 81 | 1,408,071 | 957 | 24,316,340 | 18,538 | 25,401 |
| 2875 to 3125 | 57 | 20614 | 138 | 2,681,904 | 919 | 23,571,666 | 19,400 | 25,644 |
| 3125 to 3375 | 78 | 21692 | 217 | 4,381,681 | 862 | 22,387,833 | 20,229 | 25,979 |
| 3375 to 3625 | 98 | 22770 | 314 | 6,604,300 | 783 | 20,688,056 | 21,019 | 26,408 |
| 3625 to 3875 | 112 | 23849 | 426 | 9,265,303 | 686 | 18,465,437 | 21,761 | 26,926 |
| 3875 to 4125 | 118 | 24927 | 543 | 12,105,510 | 574 | 15,803,438 | 22,445 | 27,524 |
| 4125 to 4375 | 114 | 26006 | 657 | 15,161,471 | 457 | 12,874,227 | 23,063 | 28,192 |
| 4375 to 4625 | 102 | 27084 | 759 | 17,922,976 | 343 | 9,908,266 | 23,604 | 28,920 |
| 4625 to 4875 | 84 | 28163 | 843 | 20,281,602 | 241 | 7,146,761 | 24,056 | 29,698 |
| 4875 to 5125 | 63 | 29241 | 906 | 22,121,166 | 157 | 4,788,135 | 24,416 | 30,517 |
| 5125 to 5375 | 43 | 30320 | 949 | 23,422,180 | 94 | 2,948,571 | 24,683 | 31,371 |
| 5375 to 5625 | 26 | 31398 | 975 | 24,247,950 | 51 | 1,647,557 | 24,864 | 32,254 |
| 5625 to 5875 | 14 | 32477 | 989 | 24,711,391 | 25 | 821,787 | 24,974 | 33,163 |
| 5875 to 6125 | 7 | 33555 | 996 | 24,936,881 | 11 | 358,346 | 25,032 | 34,096 |
| 6125 to 6375 | 3 | 34634 | 999 | 25,029,352 | 4 | 132,856 | 25,057 | 35,054 |
| 6375 to 6625 | 1 | 35712 | 1000 | 25,069,737 | 1 | 40,385 | 25,070* | 36,058 |

*It will be noted that this figure does not correspond exactly with that of table 49. The reason for this is that table 54 is based on the whole number of two-year-olds with a mean production of 4032.89 (see table 4) while table 49 is based on 88 of these two-year olds with a mean production of 4159.1. The corresponding total five-lactation expected records are 25,069.4 and 25,613.6.

† All calculations in this table were carried out to three decimal places, otherwise the results were found to be only approximately correct. The data however are recorded to the nearest whole number.

As the records dealt with in this paper are all for the first eight months of lactation it follows that most cows will extend beyond this limit and produce more milk. In using this table to determine what cows may be kept profitably, this fact should be kept in mind. If the dairyman has determined the complete cost of producing his milk a knowledge of the price he receives for it will allow him to determine at once from column three what cows he should keep in the herd.

### THE RELATIVE CONTRIBUTION OF ONE YEAR'S MILK PRODUCTION TO THE TOTAL PRODUCTION OVER THE FIRST FIVE LACTATIONS

A little thought on the subject will convince one that even though there is a substantial correlation between the lactation records of the individual lactation and the total production over several lactations it by no means follows that the individual cows necessarily contribute the same relative amounts of milk to the individual lactations and to the total of the five-lactation groups. The problem may be quantitatively analyzed by the determination of the correlation between the total of the five lactations of the individual cows and the deviation of the pounds of milk produced by them in the single lactations from their probable value. The calculations of this correlation may be most easily made by the method of HARRIS (1909, 1918). The formula for the correlations is given by the equation

$$r_{xz} = \frac{r_{xy} - v_x/v_y}{\sqrt{1 - r_{xy}^2 + (r_{xy} - v_x/v_y)^2}}$$

where the $y$'s represent the individual lactation records and the $x$'s the totals for the five lactations. The five constants for these are tabled in table 55.

TABLE 55

*Correlation between the total milk production of the five-lactation records and the deviation of the individual records from their probable values.*

| Age when correlation records were made | Correlation | Correlation ÷ probable error |
|---|---|---|
| 2 years and total | −0.2897 ± .0659 | 4.39 |
| 3 years and total | + .1905 ± .0693 | 2.75 |
| 4 years and total | − .0667 ± .0716 | .93 |
| 5 years and total | − .0240 ± .0719 | .33 |
| 6 years and total | + .0087 ± .0719 | .12 |

These correlations of table 55 change their sign three times, two of them being plus and three minus; their magnitudes range between $+0.1905 \pm .0693$ and $-0.2897 \pm .0659$. As adjudged by their probable errors only two of the correlations can be considered significant. Taken at their face value these coefficients would seem to indicate that the highest producers at two years contribute relatively less to the total production over several lactations than was their expected share and that these same high producers contribute relatively more in their second lactation to this total than was to be expected of them. In the other lactations each individual of a given grade contributed approximately its proportionate expected share to the total production. These relations of the deviations from their probable yields of the first and second lactations are hard to account for in terms of the known physiology of the mammary gland. The parallel already indicated of the logarithmic nature of growth and milk production with age seems to point to a possible causal relation between growth of the mammary gland and the quantity of its secretion. Should this prove true the problem of this differential relative contribution of the high producers at two years old and at three becomes a problem of the relative duration of growth of the mammary gland in the high, medium and low producers and not a cyclic action of different sets of factors for milk production itself. This means that the factors which govern milk production have their regulating power maintained in the same relative strength throughout the life of the cow with the exclusion of any group of factors acting within this life time for any short period.

## SUMMARY

The purpose of this paper is to present quantitative data, along with the biometrical analysis of the same, on the normal variations and correlations of milk production during the cow's life. The necessity of such data and analyses is well recognized now, in physiological and genetic investigations of a quantitative subject. The economic value of milk gives this investigation a significant relation to improvement in yield and in the selection of cows to remain within the herd. The materials used for this study are peculiarly suited to the ends in view. They are a strictly homogeneous group of milk records of normal pure-bred Jersey cows maintained under the conditions of a large farm, managed by a well-trained man thoroughly versed in his business. While the conclusions derived from this study are stated in general form, it is not presumed that the conclusions have more generality than the data on which

they are based. It is altogether probable however that the conclusions drawn do apply to most of the other dairy breeds of cattle.

The conclusions of most moment may be summarily stated as in the following paragraphs. Unless otherwise stated, the conclusions apply to the pure-bred Jersey herd the data for which are given in this paper.

The frequency polygons for milk production are only slightly unsymmetrical. The range of variation is large, one cow producing less than 1500 pounds in her eight-months lactation period, another cow producing more than 10,000 pounds for her eight-months lactation period. The height of the modal ordinate for the frequency polygons is greatest in the earlier and later years of the cow's life. Only one mode is evident in any of the histograms. From this it appears likely that these curves are unimodal curves. Too much stress should not be laid on this however since certain of the distributions appear quite flat-topped.

The analytical constants show that the eight-months-milk-production curves are of the PEARSON types I, II and IV. The skewness of these curves is all in the positive direction and rather small in amount. This small size of the skewness is of considerable interest to those investigators who deal with advanced-registry data since it would indicate that these data can with but small error be fitted by normal curves to determine certain of their needed constants.

The correlation coefficient between age at the commencement of test and milk production in comparison with the correlation ratio for the same variables shows that the regression of milk production on age is far from linear. This regression curve when analyzed turns out to be a logarithmic function. Attention is called to the fact that this same kind of logarithmic function also describes the relation of growth to age. This paralleling of the two functions may indicate that a causal relation exists between them such that increased milk production chiefly depends on increase in size of the mammary gland caused by growth.

The standard deviations of milk production progressing from the heifer to the aged cow are described by a cubic parabola. This regular change of the standard deviation of milk production groups shows that the curve formed by them falls into the heteroscedastic, nomic class as defined by PEARSON.

Correlation tables for milk production of the different age groups are presented.

The means derived from these tables remain, within the limits of random sampling, the same for any given age at test irrespective of the age at which the same cows were subsequently tested.

The standard deviations for the various age groups also remain at the same value within the limits of sampling irrespective of the age at which a subsequent test may be made.

As would be expected from their derivation and as actually checks out to be the case the coefficients of variation do not change within the age group for the cows which are retained in the herd for longer or shorter periods. These facts show that the cows which were kept in the herd as two-year-olds were all equally likely to be kept in the herd until they became aged cows as far as the milk production of these two-year-olds was concerned. Generalizing this statement cows which were kept in the herd at any given age were all equally likely to be kept in the herd at any other age as far as the milk record of any of those cows at the given age was concerned. This point removes any possible objection to the accuracy of the correlations for the milk productions at the various ages at least so far as concerns the cows remaining in the herd on the basis of their milk production being high.

The correlation coefficients for the milk production of one lactation with that of another lactation at another age range from $+0.2144 \pm .0919$ to $+0.7306 \pm .0284$. The signs of these correlation coefficients are all plus. The numerical values are large enough to be significant. Each set of correlation coefficients for the milk production at a given age with the milk productions at other ages in the cow's life deviate only slightly from a line which is approximately linear, taking a nearly constant value for each age. The mean value for these correlation coefficients of milk production of one lactation at any age with the milk production of another lactation at another age is $+0.5352$.

This mean value of the coefficient of correlation seems to be generally applicable to milk production for on somewhat similar data GAVIN finds results which are comparable to these.

These correlation coefficients are high for this kind of data as may be seen from the fact that correlation coefficients of similar nature for egg production range lower and have a lower mean $+0.4458$ than do these correlation coefficients for milk production.

The magnitude of these correlation coefficients in comparison to those on egg production put in terms of the physiology of the two sets of glands, mammary and ovary, means that the mammary gland works with more mechanical precision than does the ovary.

The linearity of all the regressions is established by the calculation of the correlation ratios and their comparison with the corresponding correlation coefficients.

From the means, standard deviations and correlation coefficients are formed the straight-line equations for the prediction of the amount of milk production of any given lactation at any age from these known variables at another age. These equations are given in table 43. Examination of these equations seems to show that most stress is laid on the milk production at two years old by the coefficients, indicating that the milk production at this age represents more accurately than any other the future possibilities of the cow. Similar analysis reveals the fact that correction of the milk records to about the age of maximum productivity of the cow gives the nearest approach to the correct milk production for that cow.

The correlation coefficients of milk production at a given age with the total milk production of two lactations are presented in table 46. These correlations prove to be very high, ranging from $+.7324 \pm .0286$ to $+0.9438 \pm .0116$. Such high values make it appear that the milk production of one lactation is the determining factor for total milk production of two lactations when the given lactation is one of the components.

This conclusion is confirmed by a study of a smaller series of data where the first five lactation records are known, the first commencing at two years old and the other four commencing approximately a year apart. These correlation coefficients for milk production of a lactation at a given age with the total milk production over the five lactations range from $+0.7416 \pm .0323$ to $+0.8613 \pm .0186$. Each regression is linear as is shown by a comparison of the correlation coefficients and correlation ratios.

A means of measuring the effect of environmental changes on the coefficient of correlation of the milk production of a lactation at a given age with the milk production of a lactation at another age is given. This measure depends on the difference in the correlation coefficients of the milk production of a given age correlated with the milk productions of several successive lactations and the correlation of the milk production of the given lactation and the total milk production of the other lactations. In the first case the environmental changes of the different lactations as they affect milk production make themselves felt in the correlation coefficients; in the second case the use of the total milk production gives a mean of these environmental effects. The outcome of this study shows the environmental changes reduce the correlation one-ninth to one-eighth of what it would be under the conditions of an average environment. This result makes it clear that for these Jerseys heredity

plays a greater part in their milk production from lactation to lactation than environment.

The correlation coefficients for the milk production of one lactation with that over several lactations, furnishing as it does the basis for the regression formula by which milk production over long periods may be predicted from shorter ones, is of the greatest practical importance in culling the herd of the mediocre animals. The use of these coefficients is illustrated in table 54.

The relative contribution of the different lactations to the total milk production over a long period shows that in the first lactation the high-producing cows do not produce quite as much relatively as they would be expected to produce. In the second lactation these same high-producing cows produce relatively more than they would be expected to produce. Thereafter the contribution of any class is at random. The significance of the relative contribution of the first two years is only slight. In view of these facts the conclusion may be drawn, that the factors which govern milk production have their regulatory power maintained in the same relative strength throughout the life of the cow to the exclusion of any group of factors acting within this life for any short period.

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# A GENETICAL STUDY OF FLOWER FORM AND FLOWER COLOR IN *PHLOX DRUMMONDII*

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## INTRODUCTION

Of the thousands of species of plants known to science, surely of not more than a half dozen can the student of heredity claim to have a fair knowledge. Hereditary study of the modern Mendelian sort is dependent on "the presence of differential unit characters" (SHULL 1910), and it is somewhat surprising that in the case of *Phlox Drummondii* with its large number of strains possessing marked differentiating characters no extensive analysis has yet been presented. The author has already discussed the variation in this species (KELLY 1915), having pointed out that there are forms that are tall, some that are half-dwarf, and some that are dwarf; some are large-flowered and some small-flowered; the inflorescence may be loose and spreading or rounded and dense; the flower may be single, half-double, or fully double; the fully opened flower may be salver-shaped or funnel-shaped; the colors have a wide range from

white and cream through pinks, lilacs, roses, purples and reds, to almost black; the flowers may have dark centers or eyes, or white centers; the corolla lobes may be wide and markedly overlapping or narrow; the corolla lobes may be entire or variously laciniated. One laciniate type (var. *fimbriata*) was many years ago reported to be inconstant (SPRENGER 1888). The 1914 catalogue of HAAGE and SCHMIDT, a large German seed-firm, offered for sale 173 varieties within this single species. This wealth of variation is known to have occurred subsequent to 1835, and without the aid, as far as the evidence goes, of crossing outside of the species.

Only one bit of experimental work on the genetics of *Phlox Drummondii* has thus far appeared, namely, a paper by A. W. GILBERT (1915), who carried three crosses through the $F_2$ generation, and assumed five factors to explain his observations: A dark-eye factor, a blue factor, a red factor, an intensifying factor, and a cream factor. The question of factor interactions was raised by his work, as he expressly made cream dependent on the presence of the dark-eye factor (presumably the same dark-eye factor that is necessary for the production of an anthocyanin eye); and his intensifying factor functioned visibly only when the red was present he also tacitly assumed (as the factorial formulae in his tables prove) an important interaction effect between the blue and red factors; thus in one place it appears that the blue factor alone gave rise to a lilac-colored flower, the red alone to a pink, but these two factors together were supposed to give a deep(full-)-colored carmine type. GILBERT carried none of his experiments beyond the $F_2$ generation and confirmation of his formulae is therefore lacking. A preponderance of white-flowered plants following one of his crossings was "unaccounted for."

The present paper is offered as a further contribution to the genetical analysis of the species. It is based on experimental data secured chiefly while pursuing graduate work in the Department of Biology of PRINCETON UNIVERSITY[1]; the author is indebted to Dr. G. H. SHULL, under whose auspices the work was carried on, for suggestions and an encouraging interest in the progress of the work; and to Dr. E. N. HARVEY for enlightenment on the chemical aspects of the color problems. Acknowledgments are also due to Prof. R. A. EMERSON, of CORNELL UNIVERSITY, for valuable criticisms. The paper will concern itself first with certain variations in the form of the flower; then with an analysis of color conditions in the flower.

[1] Much necessary preliminary work had been done at the PENNSYLVANIA STATE COLLEGE.

## GENETICS OF FLOWER FORM

### *The "Star Phloxes"*

In the spring of 1914 the writer sowed seeds of what the seedsman called "Star Phlox" and was impressed by the decided variation exhibited in the flowers when the plants came to maturity; one plant showed the flowers entire-edged and gave similar offspring, others bore flowers that were variously fringed or toothed. A study of the character and history of these variations was undertaken.

FIGURE 1.—To the left, a *cuspidata* plant (type L). To the right, a plant with entire-edged flowers (type A). In the center, the $F_1$ hybrid of A and L (this hybrid is of the *fimbriata* type). *Cuspidata* and *fimbriata* are "star phloxes."

As elsewhere pointed out (KELLY 1915) *Phlox Drummondii,* of which species the "Star Phloxes" are a variety or varieties, was first introduced to cultivation in 1835 and the original phloxes had entire-margined flowers. A perusal of horticultural literature published since 1835 shows that the varieties with fringed or toothed corolla segments, i.e., the "Star Phloxes," were unknown till about 1887 when they seem to have created quite a stir in German horticultural circles; in that year the firm of MARTIN GRASHOFF was awarded a certificate of merit for introducing two novelties, both of which are grouped together under the popular name of "Star Phloxes." The flowers of both novelties had fringed or incised edges. WITTMACK (1888) named these *P. Drummondii*

var. *fimbriata* and *P. Drummondii* var. *cuspidata*. On a cursory examination *cuspidata* can be distinguished from *fimbriata* by the smaller body of the flower, meaning by *body* the non-incised residuum of the

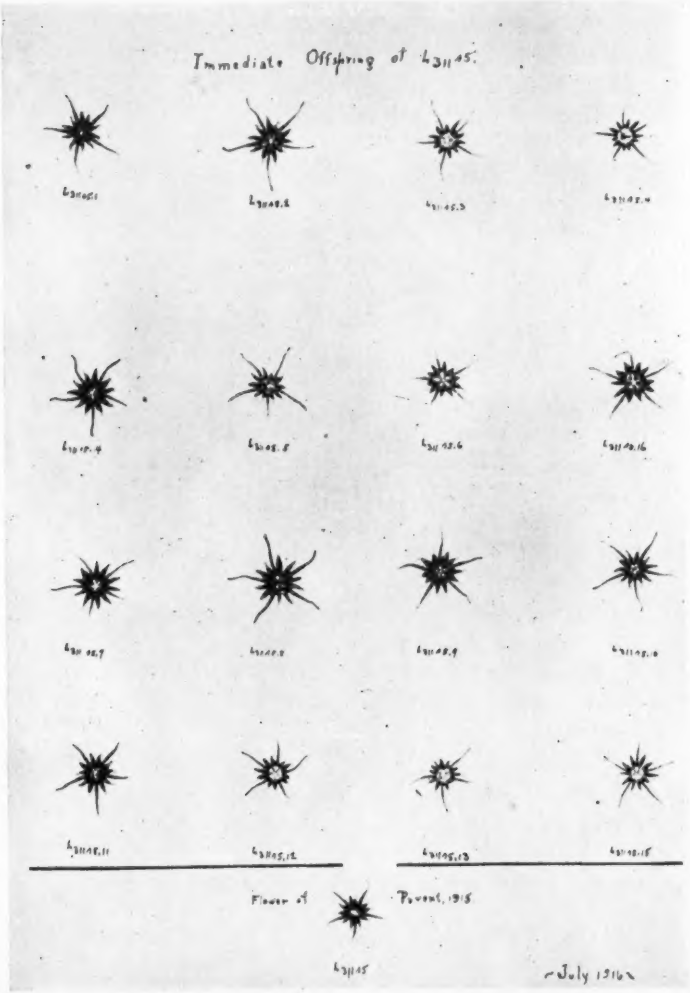


FIGURE 2.—The 16 flowers above represent a family of *cuspidata* plants; each of the 16 flowers is from a separate plant. Below, a flower from the parent of this family.

flower limb immediately surrounding the throat. Figures 2 and 5 show the contrast at a glance. This body, of course, will be in the five sections or lobes characterizing Phlox flowers of every kind; in *fimbriata* and *cuspidata,* however, each lobe bears three teeth, the middle tooth in *fimbriata* being one to four times the length of the side teeth, while in *cuspidata* it is perhaps six times the length of the side teeth.

Complete or at least a high degree of constancy through seed should ordinarily characterize a *variety* of an annual plant like *Phlox Drummondii.* A voice was soon raised against the listing of *fimbriata* as a good variety. C. SPRENGER (1888) grew plants, evidently from commercial seed, in his garden near Naples in 1888 and found but 19 *fimbriata* plants in a total of 94; he deemed this insufficient stability to warrant *fimbriata* being given varietal rank. SPRENGER assented, however, to the listing of *cuspidata* as a good variety. That these objections to *fimbriata* as a variety proved fruitless is seen from BRAND'S (1907) treatment of the Polemoniaceae in "Das Pflanzenreich." BRAND mentions both var. *fimbriata* and var. *cuspidata* in his treatment of the types of *Phlox Drummondii* and he moreover gives himself as authority for having once raised both types to full specific rank.

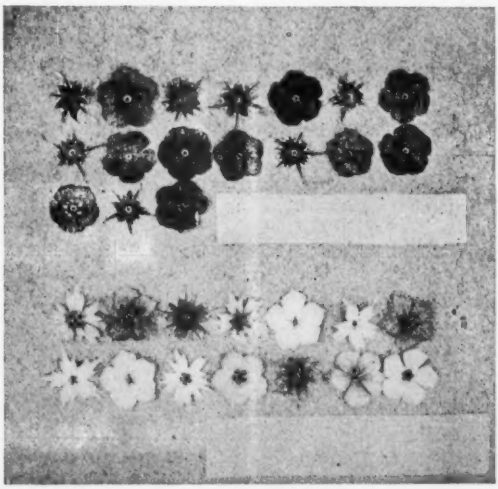

FIGURE 3.—Two families derived from back-crossing of *fimbriata* to entire. Each flower represents a single plant.

The experimental results of the writer have made clear the interrelationships of *cuspidata, fimbriata,* and the entire-edged flowers. One *cuspidata* plant of 1915 ($L_{311.5}$) was the ancestor of all the *cuspidatas* used in these experiments; there have descended directly from it, in spite of the difficulties of securing selfed seed, a total of 41 plants, all, without exception, of *cuspidata* type. Four families descended from segregate *cuspidata* plants of known hybrid extraction were also unexceptionally *cuspidata.* As far as tested, then, *cuspidata* is constant for its peculiar flower form. Figure 2 shows a flower of $L_{311.5}$ and one from each of its 16 progeny. Plants with floral periphery entire have been found to give, on inbreeding, only progeny with entire margins.

The crossing of *cuspidata* plants with those whose flowers were entire has been made in different seasons with results that have been always the same,—the $F_1$ hybrids have been of the *fimbriata* type. This particular hybridization has been made 12 times giving rise to a total progeny of 94 $F_1$ plants, all of which bore *fimbriata* flowers (see figure 1 for the parental and $F_1$ types).

On back-crossing *fimbriata* with the entire-edged type there appear only *fimbriata* and entire in about equal numbers. Several back-crosses of this kind have been made, yielding a total of 121 progeny, of which 52 were *fimbriata* and 69 bore flowers that were entire (see figure 3 and table 1).

TABLE 1

*Tabular presentation of back-crosses of fimbriata to entire.*

| Back-cross | Immediate progeny of back-cross | | | Total |
|---|---|---|---|---|
| | *Cuspidata* | *Fimbriata* | Entire | |
| Entire × $(AL)_{307}$ | 0 | 7 | 10 | 17 |
| $(AL)_{307}$ × entire | 0 | 18 | 23 | 41 |
| $(AL)_{308}$ × entire | 0 | 6 | 6 | 12 |
| Entire × $(LA)_{302}$ | 0 | 13 | 19 | 32 |
| Entire × $(GL)_{12}$ | 0 | 1 | 4 | 5 |
| Entire × *fimbriata* of commercial origin | 0 | 7 | 7 | 14 |
| Totals | 0 | 52 | 69 | 121 |

Considerable data have accumulated concerning the character of the progeny of self-fertilized *fimbriata* plants of known origin. The total number of offspring thus produced through several summers has been

706. Of these 179 bore entire flowers, 353 were *fimbriatas*, and 174 were *cuspidatas* (see table 2 and figures 6 and 7).

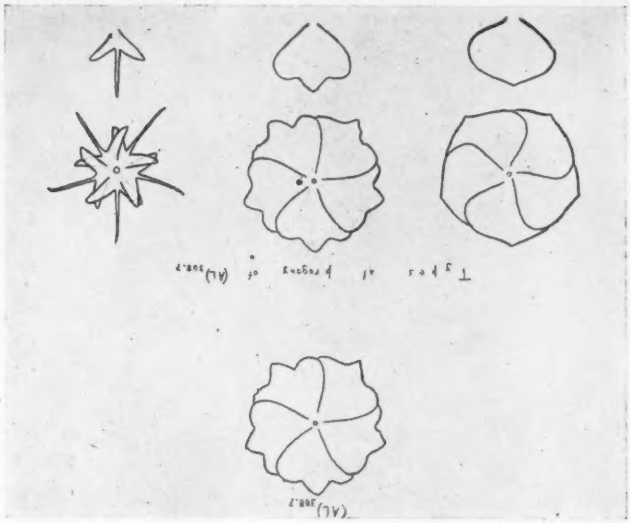

FIGURE 4.—Above, diagram of a shallowly incised *fimbriata* flower. The three flowers on the second line are diagrams of all the flower types occurring among the progeny (by selfing) of a shallowly incised *fimbriata* plant. The lowermost line gives diagrams of single corolla segments of each of the types. Compare with diagrams in figure 5 and note that shallowly laciniated plants are associated with entire-lobed sibs that are wide-lobed, and with cuspidate sibs of a peculiar type.

The experimental results set forth demonstrate very clearly that in *Pholox Drummondii* the type with entire-margined flowers differs from the *cuspidata* type by a single pair of genes; that there is a lack of dominance of the differentiating gene, which results in the production of a distinct heterozygous type called *fimbriata*; and that this $F_1$ form, *fimbriata,* can give but 50 percent of *fimbriata* offspring (25 percent being *cuspidata* and 25 percent entire) in accordance with simple Mendelian expectations. The bearing of this conclusion on the taxonomic position assigned by BRAND to *fimbriata* is obvious; *fimbriata* should not have specific rank; even varietal rank should be denied it; it should be designated as an ever-splitting hybrid form like the Blue Andalusian fowl.

Segregates from *fimbriata* plants have been tested, with results which support the general conclusion reached in the preceding paragraph.

TABLE 2
*Composition of progenies of self-fertilized fimbriata.*

| Pedigree number | Entire | *Fimbriata* | *Cuspidata* | Total |
|---|---|---|---|---|
| $(LJ)_1$ | 2 | 3 | 1 | 6 |
| $(LJ)_{100}$ | 1 | 1 | 3 | 5 |
| $(GL)_5$ | 2 | 0 | 3 | 5 |
| $(GL)_{12}$ | 5 | 8 | 6 | 19 |
| $(GL)_{12.5}$ | 3 | 9 | 5 | 17 |
| $(GL)_{12.6}$ | 3 | 3 | 1 | 7 |
| $(AL)_{221}$ | 13 | 43 | 14 | 70 |
| $(AL)_{234}$ | 6 | 9 | 4 | 19 |
| $(AL)_{308}$ | 3 | 11 | 5 | 19 |
| $(LA)_{302}$ | 19 | 25 | 12 | 56 |
| $(AL)_{307}$ | 4 | 13 | 4 | 21 |
| $(AL)_{331.65}$ | 19 | 29 | 16 | 64 |
| $[C(AL)]_1$ | 16 | 43 | 23 | 82 |
| $[B(LA)]_1$ | 11 | 26 | 10 | 47 |
| $(AL)_{331.5}$ | 1 | 2 | 2 | 5 |
| $(AL)_{308.7}$ | 13 | 21 | 11 | 45 |
| $(AL)_{161}$ | 30 | 51 | 28 | 109 |
| $[A(LA)]_1$ | 8 | 14 | 2 | 24 |
| $(AL)_{221.54}$ | 5 | 9 | 6 | 20 |
| $(AL)_{221.29}$ | 13 | 27 | 13 | 53 |
| $(AL)_{102}$ | 2 | 6 | 5 | 13 |
| Totals | 179 | 353 | 174 | 706 |

Eight entire-flowered segregates gave families averaging over 24 offspring each, every one of which bore entire-margined flowers (see figure 9). Four *cuspidata* segregates produced families averaging over 41 progeny each, every one of which was *cuspidata;* no entire flowers occurred nor any that were *fimbriata* (see figure 8).

A glance at the culture conveys the impression that the fimbriate and cuspidate flower shapes are independent of color; they can be transferred from one color type to another. A narrow white or whitish band found invariably bounding the outer edge of the *cuspidata* and *fimbriata* flowers, however, has never been found shifted to segregates with entire-edged flowers.

Concerning the variability of the types it should be said that it is to be expected in the case of any series of multiple structures like the collection of flowers on a plant that variations will occur. The flowers on a *fimbriata* plant may show fairly noticeable variation but it is not difficult to recognize a typical flower for each plant and then easily to separate the fimbriate from the cuspidate types, or types of fimbriates from one another.

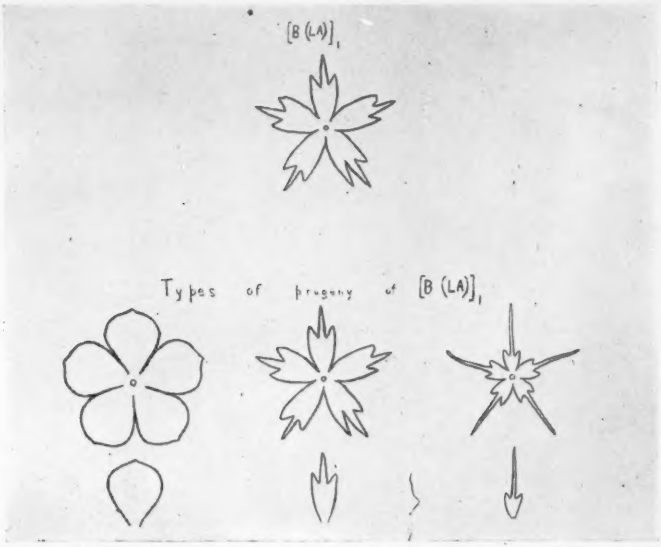


FIGURE 5.—Above is a diagram of a flower of a sharply and rather deeply incised *fimbriata* parent. The three flowers on the second line are diagrams of all the flower types appearing among its offspring. The lowermost line gives diagrams of single corolla lobes of these types. Compare with figure 4.

Some of the differences in the case of the *fimbriatas* are obviously genetic. In one $F_3$ family descended from a shallowly fringed *fimbriata* parent, designated $(AL)_{308.7}$, there were 11 *cuspidatas*, 21 *fimbriatas*, and 13 entires; all of the 21 *fimbriatas* were shallowly fringed like the parent, as shown in figures 4 and 6. The non-incised central residuum of the flower of these *fimbriatas* was nearly as extensive as the blade in the flowers of their entire sibs; the teeth were very short. An examination of the rest of the family revealed that the shallow type of *fimbriata* was associated with *cuspidata* sibs of a unique kind (see the 11 plants represented to the left in figure 6); the lateral teeth on each corolla lobe were longer and heavier than in the (typical) *cuspidata* first described, and project out more or less tangentially rather than radially; this odd type of *cuspidata* on another occasion was found to be true-breeding. Also accompanying the shallow *fimbriata* was a breadth of corolla lobe in the entire sibs that was so great that they decidedly overlapped.

Another $F_3$ family, descended from a *fimbriata* plant designated $[B(LA)]_1$, made interesting comparison with the foregoing one. It com-

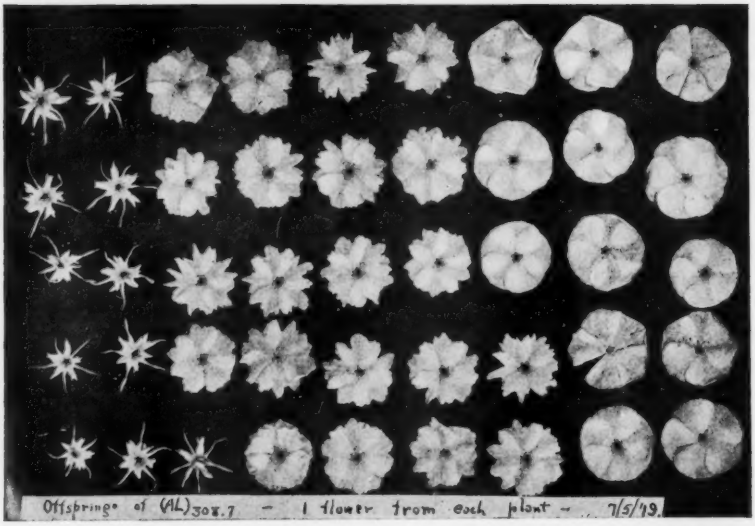


FIGURE 6.—A single family descended from a *fimbriata* parent whose flowers were shallowly incised like the fimbriates here shown. Note that the sibs of shallow *fimbriatas* are wide-lobed entires and the (new) type of *cuspidata* whose side teeth extend more or less tangentially. One flower from each plant of the family.

prised 10 *cuspidata*, 26 *fimbriatas*, and 11 entires (see figures 5 and 7). The *fimbriatas* throughout were more deeply incised and resembled their parent; the middle tooth of each corolla lobe was longer in comparison to its adjoining side teeth than was the case in the shallow *fimbriatas* discussed in the preceding paragraph. Occurring as sibs with this more incised *fimbriata* was the typical *cuspidata* whose side teeth were short and extending radially, and a narrow-lobed type of entire.

The two *fimbriata* types just described evidently differed because of some modifying factor or factors that are non-specific; these affect the condition both of the *cuspidata* and of the entire. Other families show a mixture of types.

An extreme and unusual variation arose on a portion of a single *fimbriata* plant in 1918; a few of the flowers had entire margins, these being confined to a small part of the plant which was otherwise *fimbriata*. A bud sport was suspected and seed from the entire-flowered branch was separately sown in 1919. It gave rise to 2 entire-flowered plants, 6 *fimbriata* and 3 *cuspidata* plants, and none of the *fimbriatas* again bore

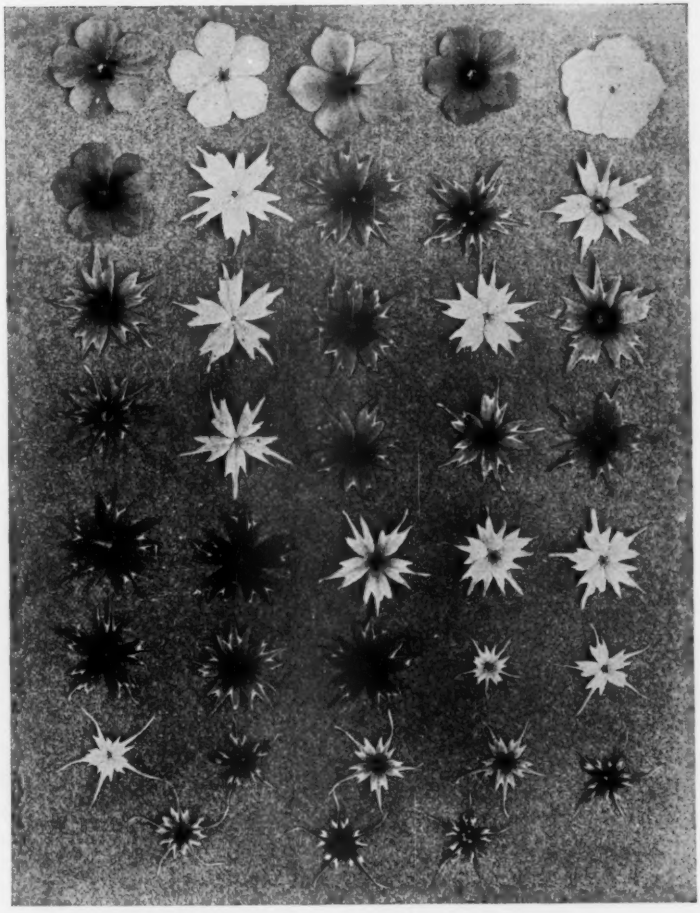

FIGURE 7.—All of the flowers of this figure represent a single family which was derived from a *fimbriata* parent of type diagrammed at top of figure 5. Each flower was from a separate plant and was typical of the plant. Attention is directed to the narrow-lobed condition of the entire flowers and to the types of the *fimbriata* and *cuspidata* sibs associated with narrow-lobed entires. (Nine sibs of these plants—5 entires and 4 *fimbriatas*—bloomed later and were not included in the photograph.)

entire flowers. The 1919 data might be taken to indicate that the variation to the entire condition was non-genetic, that it was merely a remarkably wide fluctuation. We should keep in mind, however, that the epidermis in the entire-flowered branch might have become, through a mutation or a somatic segregation in the dermatogen, genetically distinct from the other floral tissues. A constitutional change that was so localized would not be transmitted by the germ-cells of the flower since these are hypodermal in origin. The epidermis leaves no progeny, in other words, and its hereditary composition cannot be ascertained. This reservation is important since structural features normally exist in Phlox petals which point to the epidermis playing an important direct rôle in determining the flower form.

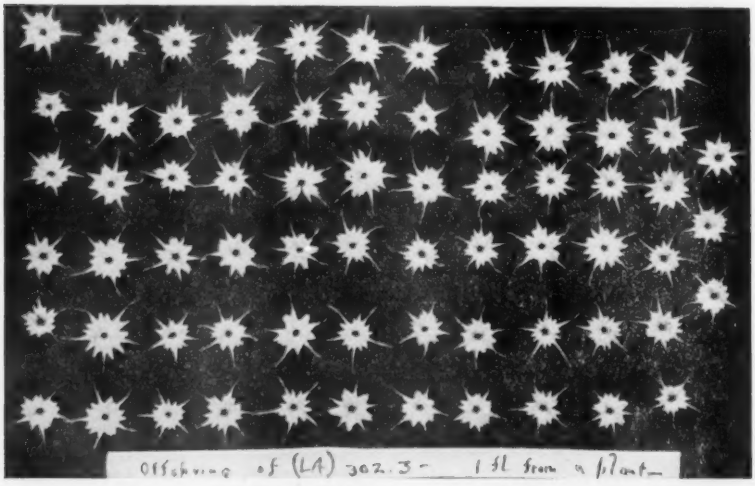


FIGURE 8.—An entire family descended from a *cuspidata* segregate. Each flower represents a separate plant and is typical for it.

## *Discussion*

It is characteristic of announcements of novelties in gardening or horticultural publications that the exact circumstances surrounding the origin of a form are omitted. The account by WITTMACK (1888) in the *Gartenflora* says that *cuspidata* arose from *fimbriata* by selection; as to how *fimbriata* arose nothing is written. The existence of *fimbriata* prior to *cuspidata* is to be noted, however; this points to the origin by mutation

of the *cuspidata* gene in a locus of a single chromosome, presenting the new mutant character in its heterozygous expression, the *fimbriata* type; and one selection among the progeny of the original *fimbriata* should have sufficed to isolate the *cuspidata*.

C. SPRENGER (1888), who seems to have been an apothecary living near Naples, claims to have seen the spontaneous origin of *cuspidata* in his garden in April, 1888, (presumably directly, without intervening *fimbriata* stage) but the statement should be accepted with reservation. SPRENGER, by his own account, had received Phlox seeds from Quedlinburg, where *cuspidata* and *fimbriata* were first presented to the trade; it seems very possible that a stray *cuspidata* seed was what gave rise to his unexpected plant. The origin of *cuspidata* directly would most probably have required two similar mutations in distinct but homologous chromosomes.

DE VRIES (1900) lists several plants which exhibit characters completely recessive in the $F_1$ hybrids and reappearing in about 25 percent of the offspring of the following generation. The laciniation or fringing of the petals of a celandine (Chelidonium) proved such a character when crossed with another celandine having entire petals.

Considering plant organs homologous with petals, some data furnished by CORRENS (1912) in nettle hybrids, by LEAKE (1911) with cotton hybrids, and by GREGORY (1911) with Primula hybrids, are pertinent. CORRENS crossed a nettle with serrated leaves and one with nearly entire leaves and found serration to be a dominant character; the $F_2$ gave a ratio of 3 serrated to 1 non-serrated. The incised nature of the floral leaves in celandine behaves as a recessive trait in hybrids; that of the foliage leaves in the nettle is a dominant trait; while the incised floral leaves of Phlox is an intermediate. LEAKE's work concerned the genetic relationship of two types of foliage leaf, both divided but differing in the degree of division; just as in Phlox, celandine, and nettle, there was found a single factorial difference; there was intermediacy in the $F_1$ generation and a clear $F_2$ segregation on a 1:2:1 basis, as in Phlox. GREGORY's (1911) results with primroses were similar to CORRENS's with the nettles; crenate leaves proved simple dominants to the non-crenate.

Viewing the experimental results in the "Star Phloxes" from the standpoint of physiological morphology, can we conceive of the possible chemical processes involved in the formation of the fringed or incised petals of *fimbriata* and *cuspidata*? This question is really one with the whole problem of the nature of the gene and the manner by which

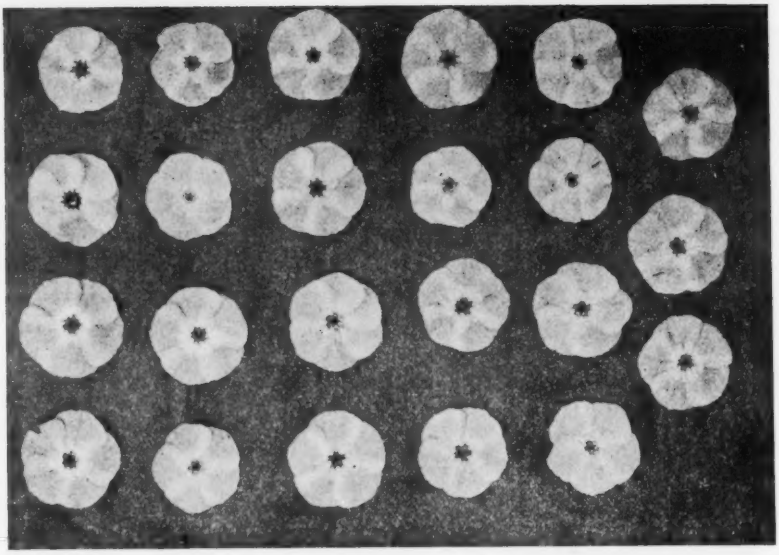

FIGURE 9.—A complete family descended from an entire-flowered segregate.

it achieves somatic expression. JENNINGS (1918), in a survey of recent genetical progress, remarks that the method of action of the genes to produce the later-appearing traits of organisms constitutes a field of research as yet little touched. Some scientists conceive the process to be enzymatic and assert that the genes are enzymes or substances which during ontogeny give rise to enzymes; that these catalyze the formation of substances distinctive chemically, which in turn are thought to form more or less directly structures or organs correspondingly distinctive. This sequence of events is a plausible one for the formation of the entire-margined flowers; it seems that in addition, in the *fimbriata* and *cuspidata* types, there is at work an inhibiting substance which retards directly the growth of the epidermal layer and to a less extent and perhaps indirectly the mesodermal layers of the petals, this retardation being less in three regions (leading to the formation of the teeth) which seem to correspond to three chief veins at the very base of the corolla lobes; the veins supply water and may be supposed to dilute the inhibitor in their vicinity, leading to tooth development. What are the reasons for assuming such an inhibitor? As pointed out before, all colored *fimbriata* and *cuspidata*

flowers display a more or less irregular, narrow, colorless margin (figure 10, C); this sort of periphery never occurred in any of the entire segregates from *fimbriata* parents. Microscopic examination of free-hand sections of corolla lobes reveals at the periphery an interesting condition. All entire flowers, pure whites as well as colored, have the typical papillated epidermal cells to the very edge of the flower, as shown in B of figure 10; color where present is confined to the papillated cells, never being found in the interior. In flowers of *fimbriata* and *cuspidata* the papillated cells do not reach the edge, as shown in A of

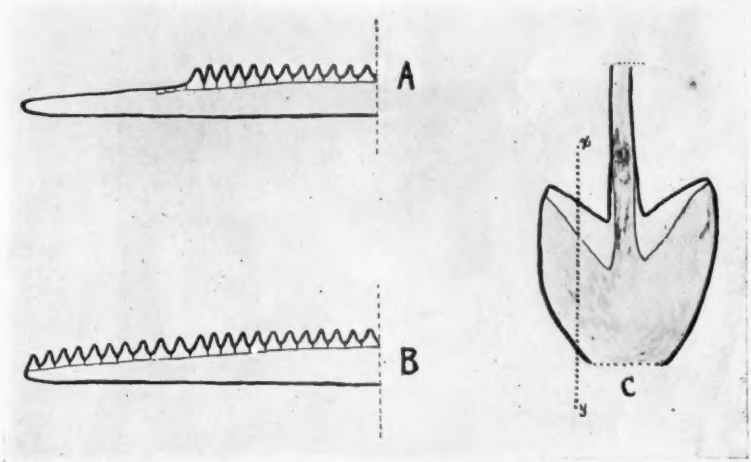


FIGURE 10.—A is diagram of the peripheral part of section of corolla lobe cut along line *xy* of C. This represents the condition in *fimbriata* and *cuspidata*. B represents a similar section of an entire-edged flower. C is a surface view of a portion of a *cuspidata* flower. Note the outer white edging of the flower.

figure 10; where the papillae cease, color also ceases and hence the white or whitish border to all the incised flowers. This border would seem to be made up of mesodermal cells that had outstripped their epidermis in growth; color production in these forms is a function of the true papillated epidermis and so does not appear in these (supposedly) uncovered mesodermal cells. The conditions described suggest the presence of a growth-inhibitor in the epidermis, which restricts the size, produces the laciniation, and the white-bordered condition in the *fimbriata* and *cuspidata* flowers.

SHULL (1912) has called attention to the occasional incompleteness of action of inhibitors; the fluctuational variation of several *fimbriata* flowers to entire, as already described, might be explained in this way. In our factorial summary we shall designate by $I_e$ the factor, which in homozygous condition, causes the cuspidate form; this symbol has reference to the fact that it is apparently an inhibitor (partial) affecting the epidermal development.

### *The funnel-shaped Phloxes*

My cultures of the funnel-shaped Phloxes were derived from seed designated commercially *"Radowitzii."* The flowers in full bloom are funnel-shaped; the first ones grown in these cultures possessed a ground

FIGURE 11.—The deep funnel type. A colored plant showing the white streaking always associated with flower color in the funnel-shaped type.

color of about a "Tyrian pink" which was streaked with white. Figure 11 shows this type of funnel-shaped Phlox; besides the characteristic shape, this type of flower commonly possesses small, irregularly distributed green streaks, and when these bits of green are at the periphery the latter becomes slightly indented. In the course of hybridization, true-breeding funnel-shaped Phloxes have arisen that are entirely white save for occasional green streakings (KELLY 1917); figure 12 is from a photograph of some of these. Other colors than "Tyrian pink" have occurred but in every case the white streaking on a colored background accompanies the funnel shape. This shape, then, as far as observations go, occurs independently of color, and always when colored is associated with white streaks on a colored ground.

My records show that selfings of 28 different funnel-shaped plants have been made at various times, giving a total of 357 progeny, and that these were unexceptionally funnel-shaped. In 1916 one family of 34 plants had its flowers only shallowly funnel-shaped; a 1917 group descended from one of these shallow-flowered plants, consisted of 20 sibs that were similarly shallow; the shallow-flowered condition is shown to the left of figure 12, while to the right is shown the commoner deep type of the writer's cultures. The hybridization work to be described was done with the latter sort (designated by an "I" in the records). All the other varieties of Phlox grown by the author had salver-shaped flowers.

The crossing between the funnel-shaped and the salver-shaped types has been made reciprocally and repeatedly. The results have always been the same; the $F_1$ hybrids show always a perfect dominance of the salver-shaped character. (Figure 13 shows the funnel-shaped and salver-shaped types to the left and right respectively, together with their $F_1$ hybrid in the centre of the picture.) Seventeen hybridizations have been made between such parents, resulting in 89 $F_1$ progeny, all salver-shaped. When color was involved in the $F_1$ hybrids the white streaking along the center of each corolla lobe proved recessive together with the funnel shape, and the irregularly distributed green streaks were likewise not apparent.

Sixteen of the $F_1$ plants were self-pollinated in different seasons, yielding a total of 713 offspring; this $F_2$ generation was composed of plants of two kinds: 534 salver-shaped and 179 funnel-shaped (see table 3). This ratio is a nearly perfect Mendelian one for a single factorial difference (with dominance).

Expectation, on this basis, would call for 534.75 salver-shaped and 178.25 funnel-shaped.

FIGURE 12.—Funnel-shaped phloxes with white flowers; shallow type to the left and deep type to the right.

In the factorial summary we shall designate by *S* the factor which, either in homozygous or heterozygous condition, causes the salver-shaped flower; and by *s* its allelomorph which, when homozygous, leads to the funnel-shaped condition.

TABLE 3

*Composition of the $F_2$ generation from crossing of the salver-shaped and funnel-shaped phloxes.*

| $F_1$ parent | $F_2$ progeny | | Totals |
|---|---|---|---|
| | Salver | Funnel | |
| $(AI)_8$ | 21 | 8 | 29 |
| $(IA)_2$ | 16 | 6 | 22 |
| $(IA)_5$ | 27 | 5 | 32 |
| $(IA)_{102}$ | 54 | 13 | 67 |
| $(IA)_{105}$ | 60 | 21 | 81 |
| $(IA)_{101}$ | 21 | 3 | 24 |
| $(IA)_{104}$ | 36 | 8 | 44 |
| $(IA)_{100}$ | 36 | 19 | 55 |
| $(IA)_{106}$ | 36 | 9 | 45 |
| $(IA)_{20}$ | 65 | 18 | 83 |
| $(AI)_{28}$ | 54 | 20 | 74 |
| $(IA)_1$ | 28 | 19 | 47 |
| $(AI)_{22}$ | 20 | 6 | 26 |
| $(AI)_{25}$ | 18 | 9 | 27 |
| $(IA)_3$ | 28 | 11 | 39 |
| $(AI)_{50}$ | 14 | 4 | 18 |
| Totals | 534 | 179 | 713 |

It has been explained already that the funnel character may be shifted about from one color type to another; it has also been evident that this character is independent of flower size, but it would seem that the larger size in funnel-shaped flowers is associated with a shallower condition. Aside from this consideration of size, however, a distinction into deeply and shallowly funnel-shaped is possible (which is genetic) as already pointed out. In the case of one plant, $(IA)_{105\cdot1}$, the flowers, even when freshly opened, were nearly salver-shaped, but possessed the occasional green streaking and peripheral notching of petals which is so common a funnel accompaniment; this plant was classified as a funnel with the provision that its final position would rest on the nature of the progeny it produced; these turned out to be undoubted funnels; this case illustrates a decided but non-hereditary variation. Another observation was



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made; flowers on old plants and sometimes old flowers on young plants may become quite salver-shaped. Not all those classed as funnel-shaped, then, possessed the deep funnel shape which characterized the types used in the crossings, but there was ordinarily no trouble in separating the two groups. No attempt was made to subdivide into deeply and shallowly funnel-shaped, but all were counted together in arriving at the figures presented in table 3.

Fifteen $F_3$ families were grown (table 4), some of which were quite small in number as lack of time prevented the making of a sufficient number of hand-pollinations. Of ten salver-shaped $F_2$ parents tested, 4

FIGURE 13.—Funnel parent type to the left; salver parent type to the right; in the center, the $F_1$ hybrid between them.

gave only salver-shaped offspring and 6 produced a mixture of salver-shaped and funnel-shaped. Theory would call for 3.33 of the true-breeding and 6.66 of the heterozygous for every 10 dominants selected at random from the $F_2$ generation. Five funnel-flowered segregates in the $F_2$ generation gave only funnel-flowered progeny in the next generation, in accordance with expectation.

TABLE 4

*Composition of the $F_3$ generation from crosses of salver and funnel phloxes.*

| Culture No. | Type of $F_2$ parent | $F_3$ progeny | | Total |
|---|---|---|---|---|
| | | Salver | Funnel | |
| $(AI)_{3.33}$ | Salver | 5 | 0 | 5 |
| $(AI)_{3.9}$ | Salver | 6 | 2 | 8 |
| $(IA)_{102.2}$ | Salver | 7 | 0 | 7 |
| $(IA)_{100.2}$ | Salver | 11 | 2 | 13 |
| $(IA)_{102.1}$ | Salver | 11 | 7 | 18 |
| $(IA)_{100.3}$ | Salver | 7 | 4 | 11 |
| $(IA)_{105.5}$ | Salver | 2 | 6 | 8 |
| $(IA)_{102.3}$ | Salver | 8 | 2 | 10 |
| $(IA)_{105.2}$ | Salver | 8 | 0 | 8 |
| $(IA)_{100.5}$ | Salver | 15 | 0 | 15 |
| $(AI)_{3.37}$ | Funnel | 0 | 19 | 19 |
| $(AI)_{3.1}$ | Funnel | 0 | 15 | 15 |
| $(IA)_{105.1}$ | Funnel | 0 | 6 | 6 |
| $(IA)_{102.7}$ | Funnel | 0 | 3 | 3 |
| $(IA)_{100.7}$ | Funnel | 0 | 38 | 38 |

The salver-shaped flower (with blade at right angles to the tube) represents the maximum (as far as observation goes) and also the normal grade of expansion in the species *Phlox Drummondii;* we have noted two hereditary grades that fall short of the salver condition, i.e., the shallow funnel and the deep funnel shown in figure 12. The extreme in this direction occurred in a single plant whose flowers did not open at all, the plant being perfectly cleistogamous. No seeds were obtained to test its heredity.

W. T. THISTLETON-DYER (1897) has pointed out that in the cultural evolution of *Cyclamen latifolium* a form arose whose corolla segments were spreading instead of being typically reflexed; this was a change in the grade of corolla expansion; nothing was reported as to the transmissibility of the new grade.

## GENETICS OF FLOWER COLOR

### *Factor differences involved when a type with completely white flowers (A) was crossed with a type having dark-eyed white-bladed flowers (B)*

### The AB series

The parental strains have been in pedigree cultures in small numbers from season to season and inbreeding has produced no non-typical speci-

mens. It should be remarked that not all completely white-flowered strains behave as the one used in the present crossing ($A_{51.16.3}$).

There were 19 $F_1$ hybrids resulting from the cross-pollination of the two parents used, six from the hybridization A × B and thirteen from the reciprocal B × A. The 19 made a decidedly uniform group, bearing flowers whose color was totally unexpected; the color of the *blade* was a full-colored type, evenly distributed, and corresponded closely with "rhodamine purple" of RIDGWAY's guide; the centre or *eye* of the flower was a more intense color. This $F_1$ group represents a case of complementary factors and the deep color produced resembles somewhat that of the flowers in the colored plate accompanying the original description of *Phlox Drummondii* by HOOKER (1835); the plants on which HOOKER based his account had been raised from seed imported from Texas, the wild habitat of the species. This $F_1$ color is much darker, however, than the color of some *Phlox Drummondii* which the author grew from seed of wild Texan plants, for which seed the author is indebted to Dr. A. B. STOUT of the N. Y. BOTANICAL GARDEN.

Six of these $F_1$ plants were bagged and furnished seed for an $F_2$ generation in 1918, consisting of 314 plants. At first glance the $F_2$ aggregation seemed a rather complex mixture of colors with pure white predominant, but a closer scrutiny revealed that nine types comprised the entire family. Eight of the types possessed color of some kind in the flowers and these eight very obviously fell into pairs, one of each pair being "bluer" than its mate.

Types Ia and Ib were both full- or deep-colored with the color uniformly distributed over the blade (flowers with such color distribution are sometimes called "self-colored"); neither possessed a narrow whitish or lighter-colored area immediately surrounding the eye. Ia had a blade color of rhodamine purple, just like the $F_1$ hybrid; Ib was the "redder" mate of Ia and had a blade color of Tyrian rose. There were 76 of type Ia and 33 of type Ib.

Types IIa and IIb also possessed a uniform distribution of their blade color (self condition), but this was much paler than in the two preceding types. The color was about "light Phlox purple" in type IIa; in its "redder" mate, IIb, the blade color was about "amaranth pink." Invariably the flowers, at least when young, possess a narrow whitish area immediately outside the eye. It is interesting to note that the IIa blade coloration is like that of the plants grown from wild seed by the writer. There were 26 IIa plants and 13 IIb plants.

Types IIIa and IIIb differ markedly from the four preceding types in the distribution of the blade color, i.e., the pigment appears to be in minute dots as though stippled on; this stippling is denser near the eye and becomes very sparse near the periphery. The pigment is also deep or full-colored. The author has fallen into the habit of calling the IIIa and IIIb plants *"duskies"* and uses this name when speaking of them in this paper. The color of the pigmented dots in the "bluer" of the "duskies" is about Rood's violet; in the "redder" of the "duskies" (IIIb) it is about Aster purple or magneta. There were 19 IIIa plants: 8 IIIb plants.

Types IVa and IVb have all color confined to an eye at the center, the blades being clear white (in the present AB series). In type IVa which resembled the "B" grandparent, the eye color is about Rood's violet, while in the "redder" member of this pair of types it is about Aster purple or magenta. There were 7 IVa plants: 2 IVb plants.

The ninth type is designated V and comprises all plants whose flowers are completely white, thus resembling the "A" grandparent. There was the unexpectedly high number of 130 plants of type V.

Colored plate 1 rather faithfully reproduces the types, together with the $F_1$ and parental types. Table 5 summarizes the $F_2$ data.

During the summer of 1919 fifty-four $F_3$ families were grown; many, however, were very small in numbers. A survey of the $F_3$ families revealed the same striking display of colors, and it was the same nine types in various proportions that made up the individual families. The color distributions are given in detail in table 6. One somewhat exceptional plant occurred in the progeny of $(AB)_{254.9}$, one of the "duskies" having the stippling dense to the very edge of the flower. The only other aberrant individual among the 889 $F_3$ plants occurred in the offspring of $(AB)_{251.7}$ where one of the IV group fell in the "a" subgroup when all were expected in IVb.

Certain features in the data of the $F_2$ and $F_3$ generations, as summarized in tables 5 and 6, should be emphasized:

a. The occurrence of a series of color types or classes. These have been designated by Roman numerals as already described. I is the darkest (full) self-colored type or class (by "self" is meant that the color is uniform in its distribution over the blade, exclusive of the eye region in this account). II is the paler self-colored type. III is the stippled "dusky" type or class. IV is the type or class with pigment confined to the eye at the center of the flower, the blade being clear white. V is the class with flowers completely white.

TABLE 5

*Flower types in the $F_2$ generation of the AB series and their observed frequencies*

| Designation of $F_2$ type | Color of flower* | | $F_2$ numbers observed |
|---|---|---|---|
| Ia ..... | Like $F_1$ type; blade about rhodamine purple | Eye *not* whitish bordered (see plate 1) | 76 |
| Ib ..... | Tyrian rose flower blade; dark eye | | 33 |
| IIa ..... | Nearly light Phlox purple; this blade resembles that of wild Phlox as grown by the writer | Eye whitish bordered (see plate 1) | 26 |
| IIb ..... | Blade between deep rose pink and amaranth pink | | 13 |
| IIIa ..... | The "bluer" stippled "dusky"; the color stippled on blade is about Rood's violet | | 19 |
| IIIb ..... | The "redder" stippled "dusky"; the color stippled on blade is about Aster purple or magenta | | 8 |
| IVa ..... | Clear white blade; eye about Rood's violet | | 7 |
| IVb ..... | Clear white blade; eye about Aster purple or magenta | | 2 |
| V ..... | Completely white | | 130 |
| | | Total | 314 |

* RIDGWAY'S "Color standards and color nomenclature" was used in color determination in this work (RIDGWAY 1912).

b. The very distinct subdivision of each color type into two subtypes marked in the tables and in the colored plate by the small letters "a" and "b". Every "a" group stands out clearly as the blue counterpart of a corresponding "b" group. This observation obviously points to a "bluing" factor capable of residing and functioning in any class of color. This independent shifting about of a gene is, of course, very characteristic of Mendelian phenomena. The absence of the "blue" factor leads to the "redder" condition.

c. The absence of forms with white eye but colored blade.

d. The theoretically very important facts that not one of the 16 $F_2$ plants of type II produced stippled "dusky" flowers, i.e., flowers of type

III, among its descendants; that no $F_2$ parent of type III on inbreeding produced any plants of type II, types II and III apparently being mutually exclusive; that type I parents are capable of producing both II and III. It would seem, then, (speaking phenotypically) that when type II meets type III it must become something else, indeed, that it must become type I. If type II were independent of type III (say epistatic to it and *not affected by its presence*) then some of the 16 $F_3$ families from type II parents should have contained type III plants and some should have lacked them; their total exclusion is significant. These observations receive strong support from the fuller data of the EF series, next to be described. Also to be noted is that type IV gives only IV or V on inbreeding and that type V produces nothing but type V. The following figures from the $F_2$ generation are of interest because of their bearing on the number of differential factors in the AB series concerned with *blade*-color formation. First, grouping type II with type I (the latter contains the differential gene for type II) we have 148 $F_2$ individuals; the total for all the other $F_2$ types (not containing the characteristic II gene) is 166; this makes a ratio of 27 : 30.2. Similarly, adding type III and type I (the latter holding the differential factor for type III we obtain 136 $F_2$ plants; all the other $F_2$ plants (not containing the characteristic "dusky" gene) total 178 individuals; this gives a ratio of 27 : 35.1. The numbers remind one more of a 27 : 37 relationship than of a 9 : 7, suggesting that a triple system of factors is prerequisite for the development of the simpler color types, i.e., types II and III.

e. The large proportion of plants with completely white flower *blades*, there being 139 in a total of 314 in the $F_2$ generation; that is, there were 175 with colored blades *of all types* and 139 white-bladed ones (some of these white-*bladed* plants had dark *eyes*), a ratio of 9 : 7.15. Roughly, this would indicate that the $F_1$ hybrids were heterozygous for two factors for blade color, these factors being so interdependent that absence of either one resulted in complete absence of blade color. Closer consideration of both the $F_2$ and $F_3$ results reveals a complication, however, which imparts considerable significance to the plus deviation of 0.15 in the second term of the ratio, giving 9 : 7.15 instead of 9 : 7 which is expected when two complementary factors are concerned. The blade color of type II is in part dependent on a factor that has no part in forming the blade color of type III, as $F_3$ results indicate; and that of type III must be due in part to a specific gene non-existent in type II. These two factors *P* and *D*, characteristic of types II and III respectively, when

LEGEND FOR PLATE I

Types of flower color which appear in the AB series. The completely white-flowered and the dark-eyed white-flowered parents represented at the top (designated by A and B respectively). Immediately below these is shown the type of the $F_1$ hybrids. The nine lowermost flowers represent the various types which appear in the $F_2$ generation. [The Editor regrets that despite his persistent efforts to secure the whiteness of the flowers of the parental and lower three $F_2$ types, the engraver has made them distinctly yellow. The colored types are nearly correct.]

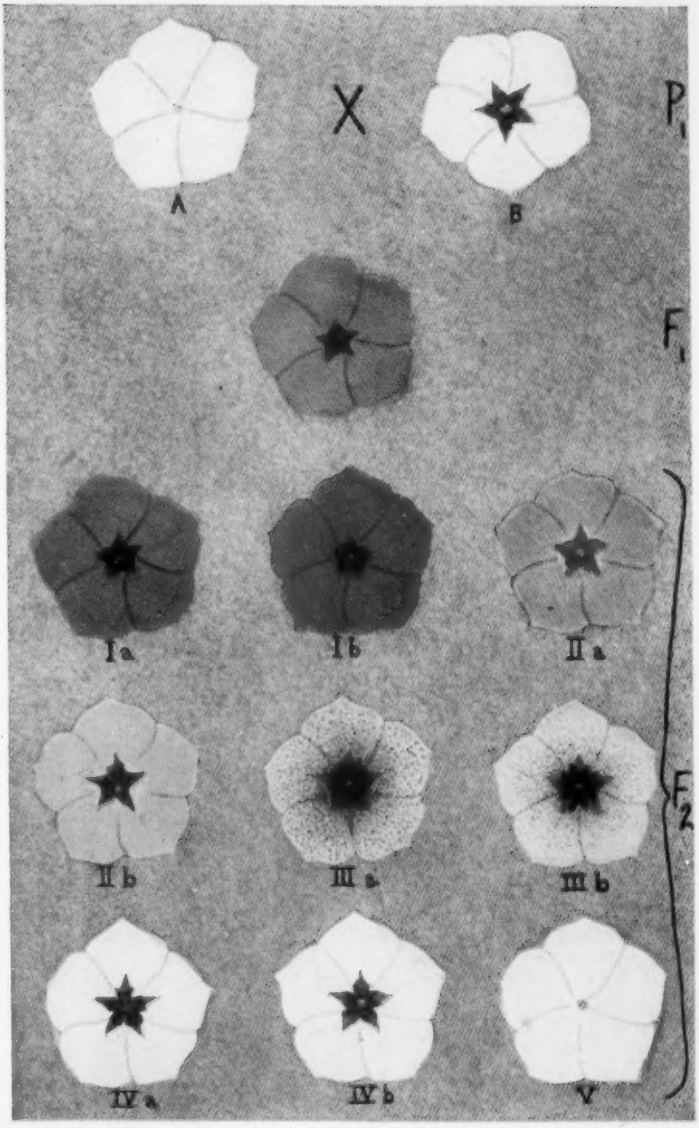

X
P1
A
B
F1
Ia
Ib
IIa
IIb
IIIa
IIIb
F2
IVa
IVb
V

TABLE 6

*Composition of the $F_3$ generation of the AB series.*

| $F_2$ parent | | $F_2$ progeny Frequencies of the several phenotypes | | | | | | | | | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Designation | Type | Ia | Ib | IIa | IIb | IIIa | IIIb | IVa | IVb | V | |
| $(AB)_{230.25}$ | Ia | 5 | 1 | 2 | — | 3 | — | — | — | 4 | 15 |
| $(BA)_{266.8}$ | Ia | — | — | 1 | — | — | — | — | — | — | 1 |
| $(BA)_{266.1}$ | Ia | 9 | — | 1 | — | — | — | — | — | 3 | 13 |
| $(BA)_{266.44}$ | Ia | 14 | 2 | 4 | 2 | 6 | — | 1 | 1 | 13 | 43 |
| $(BA)_{266.2}$ | Ia | 6 | 3 | — | — | — | — | — | — | 5 | 14 |
| $(BA)_{266.38}$ | Ia | 2 | 1 | 2 | — | 1 | — | — | — | 3 | 9 |
| $(AB)_{230.3}$ | Ia | 17 | 2 | 7 | 1 | — | — | — | — | 4 | 31 |
| $(AB)_{251.12}$ | Ia | 1 | — | 2 | — | — | — | — | — | — | 3 |
| $(AB)_{251.2}$ | Ia | 6 | 3 | 3 | — | — | — | — | — | 5 | 17 |
| $(BA)_{266.35}$ | Ia | 16 | — | 3 | — | 2 | 2 | 1 | 1 | 10 | 35 |
| $(BA)_{266.22}$ | Ia | 12 | 3 | 6 | 2 | — | — | — | — | 6 | 29 |
| $(AB)_{254.16}$ | Ib | — | 2 | — | — | — | — | — | — | — | 2 |
| $(AB)_{250.3}$ | Ib | — | 3 | — | — | — | — | — | — | 3 | 6 |
| $(AB)_{250.1}$ | Ib | — | 3 | — | 1 | — | 1 | — | — | 4 | 9 |
| $(BA)_{261.9}$ | Ib | — | 14 | — | — | — | 7 | — | — | 9 | 30 |
| $(BA)_{266.23}$ | Ib | — | 1 | — | — | — | — | — | 1 | — | 2 |
| $(BA)_{266.13}$ | Ib | — | 5 | — | — | — | — | — | — | 1 | 6 |
| $(BA)_{266.46}$ | Ib | — | — | — | — | — | 3 | — | — | 2 | 5 |
| $(BA)_{266.7}$ | Ib | — | 10 | — | — | — | — | — | — | — | 10 |
| $(BA)_{261.15}$ | Ib | — | 6 | — | — | — | 5 | — | — | 4 | 15 |
| $(AB)_{250.15}$ | Ib | — | 2 | — | — | — | — | — | — | 2 | 4 |
| $(BA)_{266.43}$ | Ib | — | 15 | — | — | — | 5 | — | — | 18 | 38 |
| $(BA)_{266.16}$ | Ib | — | 15 | — | — | — | 4 | — | — | 12 | 31 |
| $(BA)_{266.12}$ | IIa | — | — | 10 | — | — | — | — | — | 3 | 13 |
| $(BA)_{266.13}$ | IIa | — | — | 4 | — | — | — | — | — | 3 | 7 |
| $(BA)_{266.31}$ | IIa | — | — | 3 | — | — | — | — | — | 4 | 7 |
| $(AB)_{230.5}$ | IIa | — | — | 3 | — | — | — | — | — | 2 | 5 |
| $(BA)_{269.6}$ | IIa | — | — | 1 | — | — | — | 1 | — | 3 | 5 |
| $(BA)_{266.21}$ | IIa | — | — | 1 | — | — | — | 2 | — | 6 | 9 |
| $(AB)_{251.5}$ | IIa | — | — | 7 | 9 | — | — | — | — | 13 | 29 |
| $(BA)_{266.20}$ | IIa | — | — | 17 | 8 | — | — | — | — | 8 | 33 |
| $(BA)_{261.3}$ | IIa | — | — | 17 | 2 | — | — | 2 | — | 14 | 35 |
| $(AB)_{251.6}$ | IIb | — | — | — | 18 | — | — | — | 8 | 20 | 46 |
| $(BA)_{269.12}$ | IIb | — | — | — | 21 | — | — | — | — | — | 21 |
| $(AB)_{250.30}$ | IIb | — | — | — | 9 | — | — | — | — | 5 | 14 |
| $(AB)_{251.39}$ | IIb | — | — | — | 5 | — | — | — | 1 | 2 | 8 |
| $(AB)_{251.7}$ | IIb | — | — | — | 8 | — | — | — | 2 | 8 | 18 |
| $(AB)_{250.29}$ | IIb | — | — | — | 3 | — | — | — | 2 | — | 5 |
| $(AB)_{269.11}$ | IIb | — | — | — | 6 | — | — | 1 | 2 | 9 | 18 |

TABLE 6 (continued)

| $F_2$ parent | | $F_3$ progeny Frequencies of the several phenotypes | | | | | | | | | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Designation | Type | Ia | Ib | IIa | IIb | IIIa | IIIb | IVa | IVb | V | |
| $(BA)_{261.2}$ | IIIa | — | — | — | — | 21 | — | 4 | — | — | 25 |
| $(AB)_{254.9}$ | IIIa | — | — | — | — | 3 | — | — | — | 3 | 6 |
| $(AB)_{251.10}$ | IIIa | — | — | — | — | 20 | — | 5 | — | — | 25 |
| $(BA)_{260.11}$ | IIIa | — | — | — | — | 10 | — | — | — | 3 | 13 |
| $(BA)_{269.8}$ | IIIb | — | — | — | — | — | 7 | — | 4 | 11 | 22 |
| $(AB)_{254.8}$ | IIIb | — | — | — | — | — | — | — | 1 | 4 | 5 |
| $(BA)_{268.9}$ | IIIb | — | — | — | — | — | 5 | — | — | 4 | 9 |
| $(AB)_{250.8}$ | IIIb | — | — | — | — | — | 7 | — | 1 | 4 | 12 |
| $(BA)_{266.10}$ | IIIb | — | — | — | — | — | 11 | — | — | 10 | 21 |
| $(AB)_{251.20}$ | IVa | — | — | — | — | — | — | 13 | — | 11 | 24 |
| $(BA)_{260.4}$ | IVa | — | — | — | — | — | — | 7 | — | 5 | 12 |
| $(BA)_{260.8}$ | IVb | — | — | — | — | — | — | — | 12 | 5 | 17 |
| $(BA)_{266.30}$ | V | — | — | — | — | — | — | — | — | 10 | 10 |
| $(BA)_{268.6}$ | V | — | — | — | — | — | — | — | — | 16 | 16 |
| $(BA)_{269.5}$ | V | — | — | — | — | — | — | — | — | 31 | 31 |
| | | | | | | | | | | Total | 889 |

present together give type I. All blade color, in other words, is here due to the presence (among other things) of either one or both of these two factors specific for II and III, and either or both of these factors will be present in 15/16ths of the $F_2$ zygotes; for rough estimation both may be counted as single homozygous color determiners leaving the number of white-bladed plants to be determined very largely by two other independent genes, *E* and *A*, which are ineffectual unless both are present. In an exact consideration, of course, it is to be noted that 1/16th of the zygotes will lack the two genes differential for types II and III and this should add slightly to the group of white-bladed individuals, as observation actually showed. Blade color of the simplest sort, then, (that of types II or III) is dependent on three differential factors in the AB series, although the $F_2$ figures roughly support a bifactorial difference for the relationship of blade color (all sorts collectively) to lack of blade color.

With the above features of the experiments in mind we find it easy to frame a provisional hypothesis by which to interpret the data. We may

assume that three distinct factors were essential in the AB series for the appearance of either of the two simple sorts of blade color (types II and III), the absence of even one being sufficient to produce colorlessness in the blade. The most current theory concerning the formation of anthocyanin pigments is based on the work of PALLADIN and of WHELDALE (1916) and applying their conclusions to our factors we may suppose one to be a chromogen-producing factor, *P* (or *D*); the second factor, *E*, may be thought to give rise to an enzyme, possibly of the nature of an oxydase which acts on the chromogen to form anthocayanin color, provided there is present, in turn, a third factor which we may call *A* and whose function it is to produce an activator for the enzyme; this activator when fully formed might be supposed to have the constitution of an organic peroxide. When all three are present the color produced would be that of type IIb if the chromogen factor present happened to be *P*; if the chromogen factor were *D* (described below), then the color formed would be the stippled "dusky" type IIIb.

Further, we must obviously assume a factor *B* whose presence accounts for the "bluer" member of each pair of subtypes. For example in type II, the presence of this factor *B* would give type IIa, its absence, type IIb. This factor also affects the eye color, as stands out with especial clearness in type IV where no blade color is present.

A factor *D* that produces the "dusky"-appearing blade color, magenta or Aster purple, is assumed; it is conceived to give rise to an added blade chromogen; it is also conceived to be linked very closely with a factor that causes a stippled distribution of the "dusky" color. A further interesting characteristic imputed to factor *D* is that it and the factors that produce type II are complementary and give type I; speaking phenotypically we mean to say that II + III = I. More exactly expressed: *D* and *P* in the presence of *E* and *A* give the type I coloration.

Flowers of Phlox have not been chemically examined to test the assumption that multiple chromogens are present; that it is not unreasonable is attested by WHELDALE'S account (1916, page 69) of the pigments in the snapdragon; she found that the crimson and bronze varieties each contained two chromogens (flavones), i.e., apigenin and luteolin.

In Phloxes that bear completely colored flowers the pigment in the outer part of the expanded corolla (the "blade") is distinguishable from that of the central part immediately surrounding the throat (the "eye"). Variation in the species, too, has produced forms with colored blades and colorless eyes; and *vice versa*. Furthermore, proper crosses show the blade color to be segregable from the eye color. It is plausible

to suppose that the chromogen bases in the two regions are different and produced by distinct factors. The genes *P* and *D*, before described, are conceived to be concerned in chromogen production in the outer or blade part of the flower and the factor *M* is postulated for chromogen production in the eye. Since no colored-bladed white-eyed flowers occurred in this AB series the *M* must have been homozygous in these hybrids and contributed by both of the original parents. The factor *M*, in other words, is not differential in the AB series and its somatic expression as the flower eye is not particularly taken into account here; the conditions determining blade color constitute the special interest in this series.

By way of summary, the pertinent factors contained in the two plants originally crossed are listed herewith:

| PARENT $A_{51.16.8}$ | PARENT $B_{212.5}$ |
|---|---|
| *P*, chromogen factor for the IIb type of blade color. | *p*, the absence or allelomorph of *P*. |
| *e*, absence or allelomorph of *E*. | *E*, factor for an enzyme; in presence of factors for a chromogen and activator, *E* will produce anthocyanin. |
| *a*, absence or allelomorph of *A*. | *A*, factor for an activator of *E*. |
| *D*, chromogen factor for the IIIb type of color. In the AB and EF series this color is stippled on. | *d*, absence or allelomorph of *D*. |
| *b*, absence or allelomorph of *B*. The presence of *b* in homozygous condition gives the "redder" colorations. | *B*, "bluing" factor. |

M, a factor that produces the dark eye is thought to be present in both parents; if it be a chromogen-producing factor it will need the presence of both *E* and *A* for expression.

As already explained, when *P* and *D* are present together (with *E* and *A*) they interact and give a composite effect (type I).

Five independent pairs of factors are postulated in this scheme. Table 7 lists their possible combinations with the expected numbers for

TABLE 7

*The possible factor combinations for the $F_2$ generation of the AB series.*

| Factor combinations | Phenotypic formulae | Phenotype | Theoretic numbers |
|---|---|---|---|
| P E A D B | *PEADB* | Ia | 243 |
| P E A D b | *PEADb* | Ib | 81 |
| P E A d B | *PEAdB* | IIa | 81 |
| P E A d b | *PEAdb* | IIb | 27 |
| P E a D B | *PEaDB* | V | 81 |
| P E a D b | *PEaDb* | V | 27 |
| P E a d B | *PEadB* | V | 27 |
| P E a d b | *PEadb* | V | 9 |
| P e A D B | *PeADB* | V | 81 |
| P e A D b | *PeADb* | V | 27 |
| P e A d B | *PeAdB* | V | 27 |
| P e A d b | *PeAdb* | V | 9 |
| P e a D B | *PeaDB* | V | 27 |
| P e a D b | *PeaDb* | V | 9 |
| P e a d B | *PeadB* | V | 9 |
| P e a d b | *Peadb* | V | 3 |
| p E A D B | *pEADB* | IIIa | 81 |
| p E A D b | *pEADb* | IIIb | 27 |
| p E A d B | *pEAdB* | IVa | 27 |
| p E A d b | *pEAdb* | IVb | 9 |
| p E a D B | *pEaDB* | V | 27 |
| p E a D b | *pEaDb* | V | 9 |
| p E a d B | *pEadB* | V | 9 |
| p E a d b | *pEadb* | V | 3 |
| p e A D B | *peADB* | V | 27 |
| p e A D b | *peADb* | V | 9 |
| p e A d B | *peAdB* | V | 9 |
| p e A d b | *peAdb* | V | 3 |
| p e a D B | *peaDB* | V | 9 |
| p e a D b | *peaDb* | V | 3 |
| p e a d B | *peadB* | V | 3 |
| p e a d b | *peadb* | V | 1 |
| | | | 1024 |

each combination in every 1024 individuals of the $F_2$ generation; the phenotype to which each combination belongs is also indicated. In every 1024 individuals then, theory would call for 243 Ia : 81 Ib : 81 IIa : 27 IIb : 81 IIIa : 27 IIIb : 27 IVa : 9 IVb : 448 V.

Table 8 gives the theoretical expectations based on a total of 314 plants alongside of the observed results. Hypothesis leads us to expect the ratio of the more "bluish" to the more "reddish," i.e., of "a" types to "b" types, to be 3 : 1. In the $F_2$ generation, however, actual experiments gave

76 Ia : 33 Ib;
26 IIa : 13 IIb;
19 IIIa : 8 IIIb;
7 IVa : 2 IVb.

The ratio of any "a" type to any "b" type averages about 2.3 : 1. There may be some selective elimination affecting the "blue" zygotes; or, the theory of linkage may be invoked to explain this ratio, leading to the adoption of a modified view of the bluing factor. By assuming that instead of a single factor, *B*, conditioning the blue color of the classes, there are two linked genes $B_1$ and $B_2$, the presence of both of which simultaneously is necessary to give the bluish tint; and by supposing that the linkage value is 90 percent, i.e., that one crossover gamete is formed to every nine non-crossover, there would be then a ratio of "blue" to "red" of 2.3 : 1. This bifactorial interpretation for the formation of the bluish series has not been experimentally tested, either in the AB series or in the EF series next to be presented; if it be the true explanation crossings of the "red" segregates should recombine $B_1$ and $B_2$ in some of the hybrids and produce "blues," a result not to be expected on the single-factor hypothesis for bluing. The theoretical numbers in table 8 were based on a single dominant factor for bluing; these calculated numbers and the numbers observed in the experiments are repeated in table 14 (left half), together with the amended theoretical ratios, these last being based on the *pair of linked factors* for bluing just discussed. The correspondence of observation and calculation is very good. For the nine types observation furnished this ratio,—

76 : 33 : 26 : 13 : 19 : 8 : 7 : 2 : 130

while theory for the corresponding types gives about,—

69 : 29 : 23 : 9 : 23 : 9 : 7 : 3 : 137. (See table 14 for *exact* figures.)

For these ratios $\chi^2$ is about 4.3; $n'$ is 9; and by ELDERTON's table, P is .82.

In postulating a set of five independent genes to account for the genetic behavior described, the question of the number of chromosomes becomes of interest. Sections of the root-tips of seedlings reveals that there are fourteen chromosomes in the somatic cells of *Phlox Drummondii*.

In connection with the three genes considered prerequisite to any color formation, an attempt was made to describe them in terms of the chemical activities supposed to be associated with them; and the more commonly accepted of the views for the formation of anthocyanin were embodied in that factorial description. Certain investigators, however, notably COMBES, EVEREST, and WILLSTÄTTER, start from the same chromogen and arrive at anthocyanin by a different means, i.e., by a reducing

TABLE 8

*Actual and theoretical composition of the $F_2$ generation in the AB series.*

| $F_2$ phenotype | Observation | Calculation for 314 plants |
|---|---|---|
| Ia..... | 76 | 74.5135 |
| Ib..... | 33 | 24.8378 |
| IIa..... | 26 | 24.8378 |
| IIb..... | 13 | 8.2792 |
| IIIa..... | 19 | 24.8378 |
| IIIb..... | 8 | 8.2792 |
| IVa..... | 7 | 8.2792 |
| IVb..... | 2 | 2.7597 |
| V ..... | 130 | 137.3747 |
| Totals ..... | 314 | 313.9984 |

For ratios in this table $\chi^2$ is 7.6; $n'$ is 9; P is .47.

process. In the case of *Phlox Drummondii* the author has found that the water extract of white flowers, when treated with nascent hydrogen, becomes pinkish, that is, of a color in quality like that of the anthocyanin in the living flower; oxidative agencies did not achieve this result. No chemical analysis of the artificial pink pigment was made. Some reducing system may perhaps more truly represent the mechanism of color formation. It is known, for example, that methylene blue in milk becomes reduced when a little acetaldehyde is added; this is because of the presence of a reducing enzyme in the milk. To parallel this in the Phloxes we could assume a chromogen that is reduced by a reducing enzyme to an anthocyanin in the presence of some activator like an aldehyde. The substitution of this system for the one already set forth will not alter the nature of the explanation given.

An examination of table 6 shows that among the $F_3$ progeny of various Ib parents there is an unexpected dearth of plants falling in type II; an aberrant number of stippled "duskies" (type III) compared to dark-eyed whites (type IV), however, is just what would be expected on the scheme proposed, It would seem that in these cases, chiefly parents homozygous for stippled "dusky" were inadvertently chosen and the presence of factor *D* in all gametes would preclude a type II or type IV plant from appearing.

Do the experimental facts of the $F_2$ generation as summarized in table 6 bear out the hypothesis that three factors must be present before the production of either of the simpler sorts (II or III) of anthocyanin in the blade takes place? Before considering the details of the table in an

attempt to answer the question, it should be recalled that there are *two triple systems* in this AB series for production of simple blade color. These are distinguished supposedly by the chromogen factor in each. The two systems are

$$P + E + A, \text{ and}$$
$$D + E + A.$$

The $F_2$ "duskies" (type III) should give origin to $F_3$ families of three kinds, if a triple-factor hypothesis be true, depending on whether the $F_2$ parent was heterozygous for one, two, or three of the three requisite factors. With heterozygosity in just one gene there should be about one in four that is non-dusky; with heterozygosity in two of the genes there should be seven out of every sixteen offspring that are non-dusky; where an $F_2$ parent is heterozygous in all three genes there should be 37 non-dusky in every 64 offspring. Similar considerations hold in the case of $F_2$ individuals of type II. Type I, as has been pointed out, is a composite of II and III. The $F_3$ test of the hypothesis of triple systems of complementary genes for the production of the two simple types of blade color is based on a regrouping of the $F_3$ data: first, $F_2$ plants of types II and III are considered and their progeny are classified into those containing simultaneously $P$ (or $D$) $+ E + A$, and those not. It should be remembered that a stippled "dusky" (III) or a dark-eyed white (IV) lacks the factor $P$ for blade color; plants with completely white flowers lack factor $E$ or $A$ or both. When dealing with the system $P + E + A$, therefore, we must count stippled "duskies" and dark-eyed whites along with complete whites as being all without the whole set of factors for type II coloration, although another blade color may be present. The data on the groups from $F_2$ plants of types III and I bear on the second of the triple systems and the $F_3$ progeny are grouped into "dusky" or "dusky"-containing and non-"dusky." Table 9 gives the percentage of plants without $P + E + A$ simultaneously, or without $D + E + A$ simultaneously. The families with less than 15 members are omitted because of the uncertainty connected with such small numbers.

The data of table 9 are thrown together in a frequency polygon in figure 14. One $F_2$ individual, $(BA)_{269.1}$, must have been homozygous for $P$, $E$ and $A$, since no whites appeared among its $F_3$ descendants; this individual causes the small peak at 0 percent. The remainder of the curve shows three maxima; the first somewhere about 25 percent, the second near to 43.75 percent, and the third near 57.81 percent. This is in accordance with expectation on a three-factor hypothesis; for some

TABLE 9

*Data of the $F_3$ generation of the AB series regrouped to show bearing on the hypothesis of multiple factors for the production of coloration of types II and III.*

| $F_2$ parent | $F_3$ progeny | |
|---|---|---|
| | Percentage without $P+E+A$ | Percentage without $D+E+A$ |
| $(AB)_{230.25}$ | 46.6 | 40.0 |
| $(BA)_{266.44}$ | 48.8 | 48.8 |
| $(AB)_{230.2}$ | 12.9 | 38.7 |
| $(AB)_{231.2}$ | 29.4 | 47.0 |
| $(BA)_{266.33}$ | 45.7 | 42.8 |
| $(BA)_{266.22}$ | 20.6 | 48.2 |
| $(BA)_{261.9}$ | 53.3 | 30.0 |
| $(BA)_{261.13}$ | 60.0 | 26.6 |
| $(BA)_{266.43}$ | 60.5 | 47.3 |
| $(BA)_{266.16}$ | 51.6 | 38.7 |
| $(AB)_{231.5}$ | 44.8 | |
| $(BA)_{266.29}$ | 24.2 | |
| $(BA)_{261.5}$ | 45.7 | |
| $(AB)_{231.6}$ | 60.8 | |
| $(BA)_{269.12}$ | 0.0 | |
| $(AB)_{230.26}$ | 55.5 | |
| $(AB)_{231.7}$ | 66.6 | |
| $(BA)_{261.2}$ | | 16.0 |
| $(AB)_{251.18}$ | | 20.0 |
| $(BA)_{260.5}$ | | 68.1 |
| $(BA)_{266.30}$ | | 47.6 |

$F_2$ colored individuals should be homozygous for all three essential factors and be incapable of giving white descendants; some should be heterozygous in one of the factors and homozygous in the other two and behave as simple monohybrids, giving rise to 5 percent of white progeny; some should be heterozygous in two factors and homozygous in one, producing an $F_2$ ratio of 9 colored to 7 whites, in other words, give 43.75 percent of whites; the remainder should be heterozygous in all three of the necessary genes and give a ratio of 27 colored to 37 white, which amounts to 57.81 percent of white offspring.

Our calculations lead us to expect in the $F_2$ generation 27 plants containing genes for a particular blade color in every 64, on a three factor basis for this blade color; and of these 27 pigmented plants, 1 should be homozygous for all three genes, 6 should be homozygous for 2, 12 should be homozygous for one factor, and 8 should be heterozygous

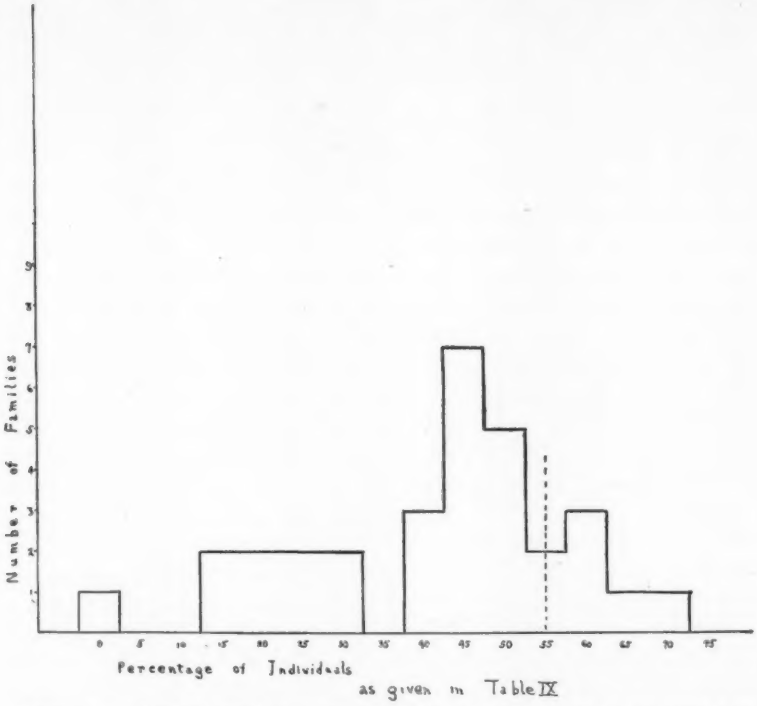



FIGURE 14.—Abscissal numbers show proportion of each $F_2$ family not containing simultaneously $P+E+A$ or $D+E+A$. Ordinates give number of families for various abscissal percentages.

for all three. Table 9 and figure 14 give experimental data on the progeny of 31 $F_2$ plants, and for this number theory would call for 1.1 : 6.8 : 13.7 : 9.1 plants of the respective genotypic constitutions just enumerated. Our observations gave for these types respectively 1 : 8 : 16 : 6, which is a fairly good correspondence with expectation. (The determination of 16 and 6 for the last two classes was obtained by arbitrarily separating the bimodal polygon constituting the right of figure 14 at the 55 percent point.)

### *Discussion of compound characters*

A brief consideration of "compound characters" (BATESON 1913, p. 60), both where the component elements are capable of independent expression and where they become visible only when present and in-

teracting, seems desirable at this point. Contributions of EAST (1912), EAST and HAYES (1911), and EMERSON (1918) have demonstrated that the simultaneous presence of as many as four distinct factors is prerequisite to the formation of aleurone color in maize. These give rise to a reddish pigmentation. The presence of a fifth (dominant) factor causes the production of a bluish coloration.

GREGORY'S (1911) work on the Chinese primrose (*Primula sinensis*) reveals an interesting similarity to the AB series just described in the Phloxes; he found that crossing full-colored kinds to a white gave an $F_2$ composed of four types: a, Full-colored selfs; b, paler-colored selfs; c, deep stippled types which he calls "Sirdars"; and d, complete whites. He did not get beyond the $F_2$ generation and left undecided the place of the paler selfs in the genetic scheme for the primrose; that is, he could not say whether the paler selfs were an independent series of colors in relation to full-colored selfs or whether they resulted "from the resolution of the combination of factors to which the full color is due." As supporting the latter alternative he pointed out that all the full-colored selfs that were crossed with a white variety called "Snowdrift" gave the paler self-colored types in the $F_2$ generation; and that two heterozygous "Sirdars" threw only "Sirdars" and whites. Concerning the "Sirdars," GREGORY considered these to differ from full-colored selfs only by a gene which made for uniform or non-stippled color distribution. There are distinct bluish and reddish subtypes of primroses but unlike the condition in the Phloxes, the "blue" is recessive to "red" and this is the situation also in *Lychnis dioica* (SHULL 1912). Data collected through the $F_3$ generation demonstrated the clear interaction-effects between the eye of the flower of primrose and the length of the style; a large diffuse eye acted as an inhibitor to the development of the long style.

The snapdragon (*Antirrhinum majus*) has been referred to as the most analyzed of plants. BAUR (1914) points out the necessity of two factors, *B* and *F*, for the production of anthocyanin of any kind. In a list of the more important factors of this plant he mentions three, *M*, $M_1$ and *L*, that intensify the color produced by *B* and *F*; he says (page 105) that a plant of the genetic formula $BBFFmmM_1M_1LL$ and one of the formula $BBFFMMm_1m_1ll$ are both of about the same color, i.e., a dark flesh color. The combination of the two with formula $BBFFMMM_1M_1LL$ is a plant that is deep velvety blackish-red ("satt sammetig schwarzrot"). This is analogous to what appears to be the

case in *Phlox Drummondii* where the combination in one plant of the factors producing the stippled "dusky" and the paler-colored selfs gives the full-colored selfs. The snapdragons have also a dominant bluing factor as in the phloxes.

In the sweet pea (*Lathyrus odoratus*) it has been long known that two factors, C and R, must be simultaneously present before any sort of anthocyanin can be formed. In addition, genetic grades of color have been described by BATESON and PUNNETT (BATESON 1913). There is the purple picotee or tinged type which differs from the deep purples by a single factor necessary for the full color of the latter. The corresponding pink picotee or tinged differs because of the same factor from the deep pinks. The condition here is not like that in the phloxes where the gene that effects an intensification of the paler self-colored types is capable of visible expression in the absence of the paler colors. The gene in sweet peas responsible for the "bluer" flower colors is a dominant one, as it is in the phloxes.

Stocks( Matthiola species) have been investigated especially by SAUNDERS (BATESON and SAUNDERS 1902; BATESON, SAUNDERS and PUNNETT 1905, 1906, 1908). Here also two factors must be present together for any anthocyanin development; a dominant bluing factor, too, is present giving rise to a "blue" and a "red" series of colors; certain light kinds, flesh-colored and lilac-colored, have appeared which are not well known from the standpoint of their relationships to each other and to the other colors. An interesting example of a compound character due to the interaction of several known genes occurs in stocks. The hairy condition is attributed to the factor *H* for hairs but this never achieves somatic expression unless the factors *C* (for cream chromogen) and *R* (for red coloration) are simultaneously present.

Among animals a classical case of a compound character and of spectacular factor interactions is that of the walnut comb in fowls (BATESON, SAUNDERS and PUNNETT 1905, 1906; also BATESON 1913). Just as in the phloxes where the resolved components of the full-colored selfs exhibited themselves independently as stippled "dusky" and paler self-colored types, so here the components of walnut comb, by themselves, attain independent expression in the form of the rose and the pea combs.

It seems needless to cite further cases. The whole trend of recent genetics is to get away from the idea of a gene independently and exclusively conditioning some "unit character" in the soma; and it is likely that factor interaction in a less spectacular manner than in the cases just discussed must be very common in the living world.

### THE CROSSING OF BRILLIANT "RED" OR CARMINE (E) BY PURE CREAM (F) —THE EF SERIES

The red parent (cultural designation $E_{47.1.1}$) and the cream parent ($F_{51.2.8}$) were both members of lines that had been the two preceding seasons in pedigree culture and known to be true-breeding for red and cream respectively. According to RIDGWAY's "Color standards and nomenclature" the cream of the blade was marguerite yellow while the red was difficult to match in that guide but it seemed to be about a brilliant pomegranate purple or carmine.

The $F_1$ generation consisted of fifteen plants that made a remarkably uniform group; the outer blade color of the flowers was very close to RIDGWAY's rhodamine purple while the eye region was deeper. The $F_1$ color seemed not so intense as that of the carmine (E) parent and it was decidedly "bluish" or purplish, indicating that the cream parent (F) had introduced both a diluting and a bluing factor.

Several of the $F_1$ individuals were selfed and gave seed for an $F_2$ generation of 530 plants, grown in 1918. The group as a whole presented a striking variety of colors ranging from some that were deeper than the $F_1$ type to those completely white. Closer scrutiny revealed *a remarkably close parallelism to the conditions already described in the AB series.* A few plants looking just like the carmine parent occurred, and also paler reddish self-colored ones, more reddish stippled duskies, reddish dark-eyed kinds (differing from their AB analogues by usually possessing a characteristic very light stippling external to the eye). For each of the types in this reddish series a closely corresponding type in a bluish series was present. Again, a large number have flowers entirely without anthocyanin. The older flowers of the "duskies," of those with color confined to the eye, and the completely non-anthocyanin forms possessed visibly either cream or white plastids; which of the other types were underlaid with cream and which with white could not be determined, as a rule, by inspection; the cream was so light that the quality of the colors of the selfs was not appreciably affected, if at all.

The visibility of cream in the lighter types was one difference setting off the EF series from the AB series. Another has also been referred to, namely, the appearance of dark-eyed forms with blades lightly stippled and which were quite distinct from the relatively heavily stippled "duskies"; the light stipples graded over into the dark-eyed forms with perfectly clear blades and the separation of the two was made with considerable difficulty and much doubt. There was also perceptible within

each main group quite minor sub-groups. When recording the $F_2$ generation the two groups of full-colored selfs whose eyes were not whitish- or lightish-bordered (Ia and Ib) and the groups of the paler-colored selfs whose eyes were always whitish- or lightish-bordered (IIa and IIb) were each subdivided into a darker and lighter subdivision; the $F_3$ observations made in 1919 indicate that a subdivision of each of the afore-mentioned groups into a darker, a medium, and a lighter would have been more in accordance with the facts; the darker of these three subdivisions (as it occurs in all of the main groups Ia, Ib, IIa, IIb) is not only darker but also "redder" than the medium and lighter ones, showing that the factor concerned here, $D_e$ is a slightly reddening as well as a slightly intensifying gene; the "lighter" subdivision is conceived as due to the minor diluting factor, $D_i$, while the medium arises when there is neither $D_e$ nor $D_i$ present. Lastly, this distinction should be emphasized, that, while the main groups among the EF and AB series are similar, in the EF series they are more intense in color. It is thought that the factors determining the color types and their relative distinctions are identical in the two groups but that they play upon a genotypic residuum in the EF series that is different from what it is in the AB series. Expressed in other words, the modifications noted in the EF series are probably due to the occurrence of one or more additional factors which have not yet been investigated.

A summary of the $F_2$ observations in the EF series is presented in table 10. No separate colored plate was furnished for the EF series since the $F_2$ types that arose so closely paralleled those of the AB series pictured in plate 1, and the same designations are used in the EF and AB series for corresponding types. This statement applies also to the type designations in the tables in these two series.

During the summer of 1919 eighty-one $F_3$ families were grown comprising a total of 3333 individuals. The EF plants were more readily self-pollinated than the AB plants, and the families therefore run larger. During 1919 the greater size of the cultures and a limitation of time prevented the subsequent follow-up examination to include late-blooming members of the families but *complete* observations on the $F_2$ generation the preceding year showed that late blooming is not associated with any particular type of flower; that late-bloomers represent a random sample of the population so far as the characters under investigation are concerned.

TABLE 10

*Flower types in the $F_2$ generation of theEF series and their observed frequencies.*

| Designation of $F_2$ type | | Color of flowers | | Observed $F_2$ numbers | |
|---|---|---|---|---|---|
| Ia | lighter | Like $F_1$ color and those close to it; blade close to rhodamine purple | No lighter area near border of eye | 103 | 131 |
| | darker | Deeper than $F_1$; blade about a brilliant Aster purple | | 28 | |
| Ib | lighter | Blade about tyrian rose | | 57 | 62 |
| | darker | Blade about bright carmine or bright pomegranate purple (= E parent type) | | 5 | |
| IIa | lighter | Blade from rhodamine purple to true purple | Eye bordered by whitish or lighter area | 59 | 73 |
| | darker | Blade perhaps between rhodamine purple and Aster purple | | *14 | |
| IIb | lighter | Blade between tyrian pink and tyrian rose | | 24 | 28 |
| | darker | Blade very close to tyrian rose | | 4 | |
| IIIa | | Stippled "dusky"; color about pansy violet or Rood's violet | | 43 | |
| IIIb | | Stippled "dusky"; color about Aster purple or magenta | | 27 | |
| IVa | stipple | Violet-eyed with relatively few stipples or dots on blade | | 14 | 28 |
| | clear | Same as last but with apparently undotted or unstippled blade | | 14 | |
| IVb | stipple | Aster purple or magenta eye and blade with sparse stippling | | 3 | 14 |
| | clear | Same as last but with apparently undotted or unstippled blade | | 11 | |
| V | white | Blade and eye completely white | | 90 | 124 |
| | cream | Blade and eye completely cream | | 34 | |
| | | | | Total | 530 |

* Four allotted to this group whose classification was somewhat doubtful.

A complete summary of the data of the $F_3$ families (together with an indication of the types of the $F_2$ parents) is given in table 11. The following features of the data of the $F_2$ and $F_3$ generations as summarized in tables 10 and 11 should be emphasized:

a. A smaller proportion of plants in this series than in the AB series whose flower blades lack anthocyanin, these having blades white or cream, or at most merely lightly stippled with anthocyanin. There were 166 such in 530, or a ratio of 1:2.19.

b. The occurrence again of a series of types of coloration just as was found in the AB series and in their larger features analogous to those found in that series.

c. The clear division again of each main group into two, a relatively "bluer" denoted by the letter "a" and a relatively "redder" denoted by "b". Certain finer sub-divisions within the groups have already been referred to.

d. As a slight variation on the AB series, this EF series contained many plants of a somewhat distinct type of blade color named by the writer *"light stipple"* which are not easily confused with the type called stippled "dusky." These "light stipples" appear like ordinary dark-eyed whites or creams whose eye color has become lightly scattered out over the blade. The parallelism to the less involved AB series allows the tracing of an analogy (homology is probably the proper word) between these two series. In individual $F_3$ families it was perfectly evident that there was the "homologue" of type I, full-colored and eye with no whitish or light area bounding it; there was the homologue of type II, slightly lighter than I but with the eye invariably possessing whitish or lighter-colored areas at its edge as in type II of the AB series (see plate 1); type III was represented in similar "duskies" that were heavily stippled; and then *just where in the AB series we look for clear-bladed dark-eyed forms (type IV) we find here, as a rule, the lightly stippled form;* the parallelism is so close in its many features that the author has not hesitated to group these "light stipples" (which are sharply distinct from the stippled "duskies") with the relatively few clear-bladed dark-eyed plants that occurred, *as type IV*, always stating, however, under IV which were "light stipples" and which were clear-bladed. It would seem, too, that plants passing as clear-bladed may be genotypically "light stipples," as was obviously the case with $(EF)_{255.6}$ (this was parent No. 74 in table 11); its $F_3$ progeny that developed color were nearly all "light stipples." The whole tendency seems to be to substitute the dark-eyed types with lightly stippled blades for the type (dark-eyed and clear-bladed)

that exclusively characterized the AB series. It is questionable whether any of the plants classified as "clear-blades" in the EF series are genotypically so; in table 11 "light stipples" and "clear blades" were separated as well as mere inspection could do this but they are put together under the general heading IV; together they are considered as equivalent to the group of the same number in table 6 and to the type of the same number pictured in plate 1. The belief was expressed above that there must be one or more uninvestigated factors working to shift all the types of blade color in the EF series toward the greater intensity they show as compared to their AB homologues; it is thought that the same uninvestigated factors also stimulate the clear-bladed forms to the greater degree of coloration evidenced in the light stippling out on the flower blade. The point to be emphasized under "d" is the apparent replacement of the clear-bladed form by the "light-stipple" form.

e. Considering the slight differences already discussed as unimportant from the present standpoint, table 11 is seen to offer a decided confirmation of a feature of table 6 that was important from the theoretical point of view: *the paler self-colored types of blade color never throw the (heavily) stippled "dusky" types and the stippled "dusky" parents never produce the paler self-colored types; the full self-colored types (Ia and Ib) give rise to both the paler self-colored (IIa and IIb) and the stippled "duskies" (IIIa and IIIb)*. The conclusion seems inevitable that (expressed phenotypically)

$$\text{type II} + \text{type III} = \text{type I}.$$

The full-colored selfs, then, are simply interaction effects of the paler-colored selfs and the "duskies"; or, the paler self-colored and the "duskies" can arise by the genetic resolution of the full-colored selfs.

Leaving out of consideration the factors that modify blade color in a very minor way we can interpret the results of crossing varieties E and F in nearly the same manner as was done for the AB series. The smaller proportion of $F_2$ plants without anthocyanin in the blade (or at most in the EF series merely lightly stippled on) indicates that the $F_1$ plants were not heterozygous for as many genes prerequisite for anthocyanin formation as in the AB series. It will be recalled that in the latter series the $F_2$ generation showed an apparent rough approximation to a ratio of 9 with blades containing anthocyanin to 7 with blades lacking it. Actually the ratio was 9:7.15 and this on analysis was shown to be due to two sets of triple complementary genes, each complete set by itself making for one of the two simple blade colors. These sets were $E + A + P$

and $E + A + D$. In the EF series the $F_2$ generation reveals a ratio of 3 plants with blades showing marked anthocyanin development to every 1.37 lacking this or at most with very light stippling on the blade. This is a rough approximation to a 3 : 1 ratio pointing to a monomeric difference between blades with anthocyanin and blades without anthocyanin. The plus deviation of the second term of the ratio, however, has a significance here that is similar to that in the AB series. The same genes *specific* for types II and III are apparently present in the EF series but only one other (whether $E$ or $A$ is purely arbitrary as far as our account goes) was differential and so heterozygous in $F_1$. Let us assume that it was gene $E$; then two simple blade color types, II and III, are present here, the former due to factors $E$ and $P$ and the latter dependent on factors $E$ and $D$. All three genes are heterozygous in the $F_1$ generation. In passing to the $F_2$ generation $P$ and $D$, either singly or together, enter 15/16 of the zygotes and so act approximately like a single homozygous gene for blade color of some sort, leaving the other gene $E$ to produce the approximately 3 : 1 ratio. It can be only *approximately* because in 1/16 of the zygotes neither $P$ nor $D$ will be present, causing a non-anthocyanous blade even though $E$ be present.

A factor which differentiates a "bluer" and a "redder" subgroup of each class must also be supposed in the EF series.

By way of summary, the following are the more important factor differences assumed:

| E PARENT | F PARENT |
|---|---|
| *b*, absence of bluing factor; gives "red" colors when homozygous. | *B*, bluing factor. |
| *P*, same as in the AB series; gene for chromogen of paler self-colored type, IIb. | *p*, allelomorph of *P*. |
| *D*, as in AB series; chromogen factor for "dusky." | *d*, allelomorph of *D*. |
| *E*, as in AB series; chromogen factor for enzyme, supposedly. | *e*, allelomorph of *E*. |

Table 12 lists the possible combinations of these factors, the expected numbers for each combination in every 256 individuals, together with the phenotype which each combination produces. Table 13 gives the theoretical expectations recalculated for 530 individuals, and places them beside the observed numbers.

TABLE 11

*Complete summary of data of $F_2$ families of $E_{21.1.1} \times F_{21.3.2}$*

| No. | $F_2$ parent, 1918 | | $F_2$ progeny, 1919 | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Full selfs | | | | | | Paler selfs | | | | | | Duskies | | | | | | | | | | |
| | Culture designation | Phenotype | Ia | | | Ib | | | IIa | | | IIb | | | IIIa | IIIb | IVa | | IVb | | V | | Total |
| | | | *Dr | M | L | Dr | M | L | Dr | M | L | Dr | M | L | Violet | Purple | Violet "Stipple" | Violet "Clear blade" | Purple "Stipple" | Purple "Clear blade" | No anthocyanin White | No anthocyanin Cream | |
| 1 | $(EF)_{234.1}$ | Ia — light | 5 | — | 1 | 1 | 1 | — | 1 | 6 | — | — | 1 | 1 | 7 | — | — | — | — | — | — | — | 17 |
| 2 | $(EF)_{234.2}$ | Ia — light | 6 | 11 | — | 1 | 8 | — | — | 7 | 2 | — | — | 3 | — | — | — | — | — | — | — | — | 38 |
| 3 | $(EF)_{234.3}$ | Ia — light | 3 | — | 5 | — | 1 | 1 | — | — | — | — | — | — | 1 | — | — | 3 | — | 1 | — | — | 7 | 22 |
| 4 | $(EF)_{234.4}$ | Ia — light | — | 11 | — | — | 2 | 2 | — | — | — | — | — | — | 3 | 1 | — | — | — | — | — | — | 19 |
| 5 | $(EF)_{233.30}$ | Ia — light | — | 6 | 7 | — | — | 4 | — | — | 4 | — | — | 2 | 3 | 1 | 1 | — | — | — | — | — | 28 |
| 6 | $(EF)_{235.40}$ | Ia — light | 6 | — | 18 | — | 2 | 5 | — | — | — | — | — | — | 5 | — | 2 | — | 2 | — | 10 | 3 | 53 |
| 7 | $(EF)_{235.42}$ | Ia — light | 5 | 1 | 11 | — | 4 | 6 | — | 2 | 1 | 1 | — | 1 | — | — | — | — | — | — | 19 | — | 51 |
| 8 | $(EF)_{235.43}$ | Ia — light | — | 7 | 30 | — | — | 11 | — | — | 7 | — | — | 5 | 6 | 3 | — | 5 | — | 2 | — | 25 | 101 |
| 9 | $(EF)_{233.42}$ | Ia — light | — | 9 | 13 | — | 2 | 10 | — | — | 1 | — | — | 1 | 6 | 2 | 2 | — | — | — | 15 | — | 61 |
| 10 | $(EF)_{234.3}$ | Ia — dark | 3 | — | — | — | — | — | 1 | — | — | — | — | — | 1 | 1 | — | — | — | — | — | 5 | 11 |
| 11 | $(EF)_{233.3}$ | Ia — dark | 6 | 6 | — | — | — | — | 2 | 6 | — | — | — | — | 1 | — | 2 | — | — | — | 3 | 1 | 27 |
| 12 | $(EF)_{233.1}$ | Ia — dark | 38 | — | — | 18 | — | — | 12 | — | — | 3 | — | — | — | — | — | — | — | — | — | 20 | 91 |
| 13 | $(EF)_{234.2}$ | Ia — dark | 34 | — | — | 21 | — | — | — | — | — | — | — | — | 20 | 10 | — | — | — | — | 20 | 4 | 109 |
| 14 | $(EF)_{234.39}$ | Ia — dark | 25 | — | — | 10 | — | — | — | — | — | — | — | — | 10 | 3 | — | — | — | — | 14 | — | 62 |
| 15 | $(EF)_{233.39}$ | Ia — dark | 11 | — | — | 8 | — | — | — | — | — | — | — | — | 12 | 5 | — | — | — | — | — | — | 36 |
| 16 | $(EF)_{235.37}$ | Ia — dark | 5 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | 6 |
| 17 | $(EF)_{235.38}$ | Ia — dark | 5 | 8 | 17 | 6 | 6 | — | — | — | — | — | — | — | 10 | 7 | 1 | — | — | — | 15 | — | 75 |
| 18 | $(EF)_{234.6}$ | — | 9 | 14 | — | 2 | 7 | — | 2 | 11 | — | 1 | 3 | — | 4 | 6 | — | 1 | — | — | 18 | 4 | 82 |
| 19 | $(EF)_{234.4}$ | Ib — light | — | — | — | — | 30 | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 5 | 37 |
| 20 | $(EF)_{234.5}$ | Ib — light | — | — | — | 14 | 53 | — | — | — | — | — | — | — | — | — | — | — | — | — | 23 | — | 90 |
| 21 | $(EF)_{234.6}$ | Ib — light | — | — | — | 4 | 13 | 2 | — | — | — | — | — | — | — | — | — | — | — | — | 13 | 1 | 33 |
| 22 | $(EF)_{234.11}$ | Ib — light | — | — | — | 6 | 12 | — | — | — | — | — | — | — | — | 3 | — | — | — | — | — | 11 | 32 |
| 23 | $(EF)_{235.32}$ | Ib — light | — | — | — | 1 | 7 | — | — | — | — | 2 | 4 | — | — | — | — | — | — | — | 3 | 3 | 20 |
| 24 | $(EF)_{234.38}$ | Ib — | — | — | — | 5 | 7 | — | — | — | — | 2 | 7 | — | — | 9 | — | — | — | 2 | 13 | — | 45 |
| 25 | $(EF)_{235.3}$ | Ib — | — | — | — | — | 2 | — | — | — | — | — | 5 | — | — | — | — | — | 2 | — | — | 4 | 13 |
| 26 | $(EF)_{235.1}$ | Ib — dark | — | — | — | 4 | 1 | — | — | — | — | 2 | 2 | — | — | 4 | — | — | — | — | — | — | 13 |
| 27 | $(EF)_{236.39}$ | Ib — dark | — | — | — | 26 | — | — | — | — | — | 15 | — | — | — | 8 | — | — | 8 | — | — | — | 57 |
| 28 | $(EF)_{234.8}$ | IIa — light | — | — | — | — | — | — | 3 | 10 | — | 2 | 6 | — | — | — | 3 | 2 | — | 1 | — | — | 27 |
| 29 | $(EF)_{234.6}$ | IIa — light | — | — | — | — | — | — | 2 | — | 25 | — | — | 5 | — | — | — | — | — | — | — | — | 32 |
| 30 | $(EF)_{235.29}$ | IIa — light | — | — | — | — | — | — | 7 | — | 16 | 4 | — | 3 | — | — | 4 | 3 | — | 1 | 1 | 3 | 42 |
| 31 | $(EF)_{236.11}$ | IIa — light | — | — | — | — | — | — | — | 2 | 22 | 1 | 2 | 17 | — | — | 16 | — | 5 | — | — | 20 | 85 |
| 32 | $(EF)_{236.15}$ | IIa — light | — | — | — | — | — | — | 4 | 19 | — | 2 | 8 | — | — | — | 5 | 4 | 2 | 2 | 8 | 1 | 55 |
| 33 | $(EF)_{236.16}$ | IIa — light | — | — | — | — | — | — | — | — | 29 | — | — | 14 | — | — | 13 | 1 | 1 | 2 | — | 19 | 79 |
| 34 | $(EF)_{235.32}$ | IIa — light | — | — | — | — | — | — | 4 | 7 | — | — | — | — | — | — | 3 | — | — | — | 2 | — | 16 |
| 35 | $(EF)_{235.37}$ | IIa — | — | — | — | — | — | — | — | 10 | — | — | 1 | — | — | — | 2 | — | — | — | — | — | 13 |
| 36 | $(EF)_{234.39}$ | IIa — light | — | — | — | — | — | — | 5 | — | 39 | 1 | — | 5 | — | — | — | — | — | — | — | 7 | 57 |
| 37 | $(EF)_{234.41}$ | IIa — light | — | — | — | — | — | — | 4 | — | 8 | 4 | — | 2 | — | — | 2 | 5 | 2 | 2 | — | 12 | 41 |
| 38 | $(EF)_{235.8}$ | IIa — | — | — | — | — | — | — | 6 | 15 | — | 4 | 7 | — | — | — | 2 | 1 | 4 | — | 12 | 2 | 53 |
| 39 | $(EF)_{235.39}$ | IIa — | — | — | — | — | — | — | 8 | 8 | 8 | — | — | — | — | — | — | — | — | — | 2 | 4 | 30 |
| 40 | $(EF)_{235.39}$ | IIa — | — | — | — | — | — | — | — | 17 | 18 | — | 3 | 14 | — | — | 13 | — | 2 | — | — | — | 67 |
| 41 | $(EF)_{236.39}$ | IIa — | — | — | — | — | — | — | 34 | — | — | 18 | — | — | — | — | — | — | — | — | — | — | 52 |
| 42 | $(EF)_{236.6}$ | IIa — dark | — | — | — | — | — | — | 23 | — | — | 9 | — | — | — | — | 5 | — | 1 | — | — | — | 38 |
| 43 | $(EF)_{235.39}$ | IIa — doubtful | — | — | — | — | — | — | 8 | — | — | 3 | — | — | — | — | 2 | — | 1 | — | — | 3 | 17 |

* Dr=darker; M=medium; L=lighter.

TABLE 11 (continued)

*Complete summary of data of $F_2$ families of $E_{11.11} \times F_{11.29}$*

| No. | $F_2$ parent, 1918 | | $F_3$ progeny, 1919 | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Full selfs | | | | | | Paler selfs | | | | | | Duskies | | | | | | |
| | | | Ia | | | Ib | | | IIa | | | IIb | | | IIIa | IIIb | IVa | | IVb | | V | | |
| | Culture designation | Phenotype | *Dr | M | L | Dr | M | L | Dr | M | L | Dr | M | L | Violet | Purple | Violet "Stipple" | Violet "Clear blade" | Purple "Stipple" | Purple "Clear blade" | No anthocyanin White | No anthocyanin Cream | Total |
| 44 | $(EF)_{251.5}$ | IIb — light | — | — | — | — | — | — | — | — | — | — | — | 10 | — | — | — | — | 2 | — | — | — | 12 |
| 45 | $(EF)_{250.3}$ | IIb — light | — | — | — | — | — | — | — | — | — | 12 | 44 | — | — | — | — | — | 10 | — | 34 | — | 100 |
| 46 | $(EF)_{250.24}$ | IIb — light | — | — | — | — | — | — | — | — | — | — | — | 51 | — | — | — | — | 19 | 1 | 18 | 5 | 94 |
| 47 | $(EF)_{254.26}$ | IIb — light | — | — | — | — | — | — | — | — | — | — | 4 | 19 | — | — | — | — | 2 | 6 | 7 | 1 | 39 |
| 48 | $(EF)_{252.16}$ | IIb — | — | — | — | — | — | — | — | — | — | — | 8 | 24 | — | — | — | — | 18 | 4 | 6 | 2 | 64 |
| 49 | $(EF)_{255.23}$ | IIb — dark | — | — | — | — | — | — | — | — | — | 23 | — | — | — | — | — | — | 9 | — | — | — | 32 |
| 50 | $(EF)_{252.2}$ | IIb — dark | — | — | — | — | — | — | — | — | — | 25 | — | — | — | — | — | — | 12 | — | 10 | 3 | 50 |
| 51 | $(EF)_{254.8}$ | IIIa — "dusky" | — | — | — | — | — | — | — | — | — | — | — | — | 22 | — | — | — | — | — | 5 | — | 27 |
| 52 | $(EF)_{252.12}$ | † | — | — | — | — | — | — | — | — | — | — | — | — | 6 | — | — | — | — | — | 1 | 1 | 8 |
| 53 | $(EF)_{255.26}$ | IIIa — "dusky" | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — | 1 |
| 54 | $(EF)_{255.27}$ | IIIa — "dusky" | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | — | 2 |
| 55 | $(EF)_{255.28}$ | IIIa — "dusky" | — | — | — | — | — | — | — | — | — | — | — | — | 35 | — | 10 | — | — | — | 10 | 9 | 64 |
| 56 | $(EF)_{256.28}$ | IIIa — "dusky" | — | — | — | — | — | — | — | — | — | — | — | — | 7 | 4 | 2 | — | 2 | — | — | — | 15 |
| 57 | $(EF)_{253.17}$ | IIIa — "dusky" | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | 3 | — | — | — | 2 | — | 6 |
| 58 | $(EF)_{254.14}$ | IIIa — "dusky" | — | — | — | — | — | — | — | — | — | — | — | — | 13 | — | 4 | — | — | — | — | 4 | 21 |
| 59 | $(EF)_{260.8}$ | IIIb — "dusky" | — | — | — | — | — | — | — | — | — | — | — | — | — | 50 | — | — | — | — | — | — | 50 |
| 60 | $(EF)_{253.13}$ | IIIb — "dusky" | — | — | — | — | — | — | — | — | — | — | — | — | — | 17 | — | — | — | — | 10 | 1 | 28 |
| 61 | $(EF)_{254.13}$ | IIIb — "dusky" | — | — | — | — | — | — | — | — | — | — | — | — | — | 38 | — | — | — | — | — | — | 38 |
| 62 | $(EF)_{254.23}$ | † | — | — | — | — | — | — | — | — | — | — | — | — | — | 47 | — | — | 11 | 1 | — | 23 | 82 |
| 63 | $(EF)_{254.19}$ | † | — | — | — | — | — | — | — | — | — | — | — | — | — | 35 | — | — | — | — | 5 | 4 | 44 |
| 81 | $(EF)_{254.30}$ | IIIb—"dusky" | — | — | — | — | — | — | — | — | — | — | — | — | — | 5 | — | — | — | — | — | — | 5 |
| 64 | $(EF)_{251.8}$ | IVa—"stipple" | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 25 | — | 7 | — | — | — | 32 |
| 65 | $(EF)_{253.7}$ | IVa—"stipple" | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 7 | — | — | — | — | — | 7 |
| 66 | $(EF)_{258.18}$ | IVa—"stipple" | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 10 | — | 9 | — | 7 | — | 26 |
| 67 | $(EF)_{259.10}$ | IVa—"stipple" | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 54 | 1 | — | — | — | 9 | 64 |
| 68 | $(EF)_{255.11}$ | IVa—"stipple" | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 42 | — | 9 | — | — | — | 51 |
| 69 | $(EF)_{258.15}$ | IVa—"stipple" | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 16 | — | — | — | — | — | 16 |
| 70 | $(EF)_{255.25}$ | IVa—"stipple" | — | — | — | — | — | — | — | — | — | — | — | 13 | — | — | 7 | — | 3 | — | — | — | 13 |
| 73 | $(EF)_{261.11}$ | IVa—"clear blade" | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 15 | 23 | 12 | 3 | 10 | — | 63 |
| 71 | $(EF)_{255.14}$ | IVb—"stipple" | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 45 | — | — | — | 45 |
| 72 | $(EF)_{255.15}$ | IVb—"stipple" | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 25 | 1 | — | 7 | 33 |
| 74 | $(EF)_{255.5}$ | IVb—"clear blade" | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 40 | 3 | 17 | — | 60 |
| 75 | $(EF)_{255.19}$ | IVb—"clear blade" | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 7 | 12 | 5 | 2 | 26 |
| 76 | $(EF)_{256.17}$ | IVb—"clear blade" | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 11 | 23 | — | 12 | 46 |
| 77 | $(EF)_{261.14}$ | V — all white | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 21 | — | 21 |
| 78 | $(EF)_{260.1}$ | V — all white | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 43 | — | 43 |
| 79 | $(EF)_{256.15}$ | V — all cream | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 18 | 18 |
| 80 | $(EF)_{252.30}$ | V — all cream | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 45 | 45 |
| | | | | | | | | | | | | | | | | | | | | | Total = | | 3333 |

* Dr=darker; M=medium; L=lighter.

† The record of 1918 for $(EF)_{262.12}$ $(EF)_{251.16}$ and $(EF)_{251.16b}$ fails to state whether those were stippled "dusky" or "light stipple."

§ These three construed as due to foreign pollen.

TABLE 12

*The possible combinations of the chief factors in the $F_2$ generation of the EF series.*

| Factor combinations | Phenotypic formulae | Phenotype | Theoretical numbers |
|---|---|---|---|
| $P$ { $E$ { $D$ { $B$ | *PEDB* | Ia | 81 |
| $P$ { $E$ { $D$ { $b$ | *PEDb* | Ib | 27 |
| $P$ { $E$ { $d$ { $B$ | *PEdB* | IIa | 27 |
| $P$ { $E$ { $d$ { $b$ | *PEdb* | IIb | 9 |
| $P$ { $e$ { $D$ { $B$ | *PeDB* | V | 27 |
| $P$ { $e$ { $D$ { $b$ | *PeDb* | V | 9 |
| $P$ { $e$ { $d$ { $B$ | *PedB* | V | 9 |
| $P$ { $e$ { $d$ { $b$ | *Pedb* | V | 3 |
| $p$ { $E$ { $D$ { $B$ | *pEDB* | IIIa | 27 |
| $p$ { $E$ { $D$ { $b$ | *pEDb* | IIIb | 9 |
| $p$ { $E$ { $d$ { $B$ | *pEdB* | IVa | 9 |
| $p$ { $E$ { $d$ { $b$ | *pEdb* | IVb | 3 |
| $p$ { $e$ { $D$ { $B$ | *peDB* | V | 9 |
| $p$ { $e$ { $D$ { $b$ | *peDb* | V | 3 |
| $p$ { $e$ { $d$ { $B$ | *pedB* | V | 3 |
| $p$ { $e$ { $d$ { $b$ | *pedb* | V | 1 |

It must be admitted that the calculations in table 13 show theory and observation to be not exceedingly close fits. In view of the relationship of "dusky" (III), the paler self-colored (II), and the full-colored (I) types, elsewhere emphasized, it is interesting to note that a deficiency of the violet "duskies" (IIIa) is accompanied by a deficiency of the "bluer" full-colored selfs (Ia) but with an excess of the paler "bluish" selfs (IIa); some single cause affecting adversely the appearance of violet dusky gametes would bring about simultaneously the other two deviations from the expected.

TABLE 13

*Actual and theoretical composition of the $F_2$ generation of the EF series.*

| $F_2$ phenotype | Observed frequencies | Theoretical frequencies for 530 plants |
|---|---|---|
| Ia | 131 | 167.67 |
| Ib | 62 | 55.89 |
| IIa | 73 | 55.89 |
| IIb | 28 | 18.63 |
| IIIa | 43 | 55.89 |
| IIIb | 27 | 18.63 |
| IVa | 28 | 18.63 |
| IVb | 14 | 6.21 |
| V | 124 | 132.48 |
| Total | 530 | 529.92 |

† The record of 1918 for $(EF)_{22.8}$ and $(EF)_{20.10}$ fails to state whether those were stippled "dusky" or "light stipple."
§ These three construed as due to foreign pollen.

Let us once more consider the ratio of "blues" to "reds" (i.e., any "a" subgroup to its "b" mate),—this time in both tables 5 and 10; and of the ratio of "blues" to "reds" among the progeny of heterozygous "a" parents for the main groups of the $F_3$ generation of the EF series (as summarized in table 11). It becomes evident that the ratio is not 3:1 as expected on our assumption but averages again about 2.3:1. This may be due, as remarked above, to some sort of selective elimination of the "blue" zygotes; but of the "blues" which survive the author cannot assert that they are weaker than the "reds." The theory of linkage has been invoked already to explain this ratio, by assuming that instead of a single factor, *B*, conditioning the "blue" colors of the classes, there are two linked genes, $B_1$ and $B_2$, the presence of both of which simultaneously is necessary for "blue" formation; and by supposing that the linkage value is 90 percent. The theoretical ratios first proposed for the AB and EF series (see tables 8 and 13) were based on a single dominant factor; those calculations and the numbers actually observed in the experiments in both series are repeated in table 14, together with the amended theoretical ratios, these last being based on the *pair of factors* for "bluing" just discussed. In the EF series the square of chi ($\chi^2$) is much reduced by the bifactorial hypothesis for "bluing," but the value of P remains still very small.

TABLE 14

*A comparison of two hypotheses concerning the relation of the bluish to the reddish subgroup.*

| Type | AB series | | | EF series | | |
|---|---|---|---|---|---|---|
| | Observation | Theoretical 1 *B* gene | Theoretical 2 *B* genes | Observation | Theoretical 1 *B* gene | Theoretical 2 *B* genes |
| Ia | 76 | 74.51 | 69.54 | 131 | 167.67 | 156.49 |
| Ib | 33 | 24.83 | 29.80 | 62 | 55.89 | 66.07 |
| IIa | 26 | 24.83 | 23.18 | 73 | 55.89 | 52.16 |
| IIb | 13 | 8.27 | 9.93 | 28 | 18.63 | 22.36 |
| IIIa | 19 | 24.83 | 23.18 | 43 | 55.89 | 52.16 |
| IIIb | 8 | 8.27 | 9.93 | 27 | 18.63 | 22.36 |
| IVa | 7 | 8.27 | 7.73 | 28 | 18.63 | 17.38 |
| IVb | 2 | 2.75 | 3.31 | 14 | 6.21 | 7.46 |
| V | 130 | 137.37 | 137.37 | 124 | 132.48 | 132.48 |
| | 314 | $\chi^2 = 7.6$ P = .47 | $\chi^2 = 4.3$ P = .82 | 530 | $\chi^2 = 40$ P less than .01 | $\chi^2 = 29$ P also very small |

At the present stage of investigation it is not meant to urge this bifactorial hypothesis for bluing; it is offered simply as a suggestion. The obtaining of "blues" from matings of extracted "reds" would offer substantiation of the hypothesis, as already pointed out; there should be corroboration also in those $F_3$ families descended from heterozygous ($F_2$) parents of the Ia, IIa, IIIa, and IVa groups; some of these parents (about one in every eleven) should be heterozygous in just one of the pair of linked bluing factors due to their holding one crossover and one non-crossover chromosome, and such should furnish about 25 percent of "red" progeny; those heterozygous for the two should give 29 or 30 percent of "reds." The percentage of "reds" in the $F_3$ families of the large EF series has been calculated and the data form the frequency polygon shown in figure 15 (families comprising less than 15 colored individuals are omitted). There is some evidence of a peak at about

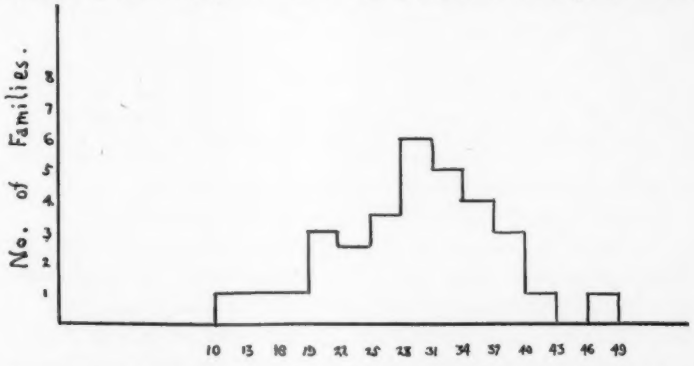



FIGURE 15.—Abscissal numbers show proportion in percent of each $F_3$ family that is reddish; ordinates give number of families for various abscissal values.

21 percent (expected 25 percent); the high peak at about 29 percent is as expected. Further experimental data are needed to settle the matter.

## THE CROSSING OF WHITE-EYED PINK (J) AND COMPLETELY WHITE (A)—THE JA SERIES

The J parent was one of 26 sibs resulting from the guarded pollination of a plant of commercial origin; all 26 were similar to one another. Each flower had a white eye as a center, surrounded on the outer blade by a color that was close to the eosin pink of RIDGWAY'S guide. The white parent was one of a line that had been observed in pedigree culture for two seasons and had been found to be giving only whites.

The particular pair of plants used as parents were crossed reciprocally giving five similar offspring; the color of the flower of these $F_1$ hybrids was a complete surprise; they were dark-eyed and the outer blade was one of the full colors, tyrian rose. Three of the plants furnished seed for an $F_2$ generation of 217 plants. Nine types of flower actually occurred among the descendants of the hybrids of J and A, but only eight of these were recorded as occurring in the $F_2$ generation. Plate 2 shows in

TABLE 15

*Flower type in the $F_2$ generation of the JA series with their observed and calculated frequencies.*

| Type | Color of type | Observed numbers in $F_2$ | Theoretical numbers for $F_2$ |
|---|---|---|---|
| Ia | Dark-eyed; blade tyrian rose or bright pomegranate purple; like $F_1$ | 64 | 68.6 |
| Ib | White-eyed; blade between tyrian rose and tyrian pink | 20 | 22.8 |
| IIa | Dark-eyed; blade like next type (IIb) but a trifle darker | 34 | 22.8 |
| IIb | White-eyed; blade about eosin pink; like J parent | 13 | 7.6 |
| IIIa | Dark-eyed; blade about Aster purple or magenta (= non-stippled "dusky") | 23 | 22.8 |
| IIIb | White-eyed; blade near mallow pink and stippled | 9 | 7.6 |
| IV | Completely white; like A parent | 48 | 54.2 |
| Va | Dark-eyed; blade about deep rose pink | 6 | 7.6 |
| Vb | White-eyed; color usually confined to small single arrow-shaped spot on each corolla lobe | 0 | 2.5 |
| | Total | 217 | 216.5 |

NOTE.—In tables 15 and 16 the distinction between any "a" group and its corresponding "b" group is *not* as in the EF and AB series, a matter of a bluing factor; in the JA series any "a" group is distinguished from its "b" by a factor for dark-eye; this point will be presently discussed. By ELDERTON's tables, P for the data above is about .10.

colors the types of the parents, of the $F_1$ generation and of the $F_2$ generation; Type Vb, not reported among the $F_2$ experimental results, is pictured among the colored $F_2$ types, since it is believed that because of the exceedingly small amount of color, even when well developed, and of the fluctuability of what little there is (potentially), that Vb *may* have occurred and was counted among the completely white; by the hypothesis to be developed, however, it is expected in only .8 of one percent of the cases and it may not have occurred at all because of the small number of experimental plants, 217. Table 15 summarizes all of the $F_2$ data.

Within the more deeply colored of the groups some quite minor variations in the depth of pigmentation were in evidence; these were not selected as the basis for further division, since $F_3$ results showed that they continued of minor importance. The types as given in table 15 were sharply distinct except sometimes in the following cases: light forms of type IIa very much resembled Va plants; a slight bluish tinge in the latter which increased with the aging of the flowers would usually separate doubtful cases, but even this did not prevent one obvious misclassification: $(JA)_{11.91}$ was given as Va in 1918 but by progeny test in 1919 it was shown to have been a lighter IIa plant. In type Vb color is confined as a rule to a single small arrow-shaped spot on each lobe (see plate 2); the color is light and often barely perceptible when it may be easily overlooked and the flower rated as completely white.

During the summer of 1919 thirty-two $F_3$ families were grown, comprising a total of 1518 individuals. Table 16 presents a summary of data, giving to the left the phenotype of the $F_2$ parent and in the body of the table the character of the ($F_3$) offspring.

The following points of $F_2$ and $F_3$ generations (as summarized in tables 15 and 16) should be emphasized:

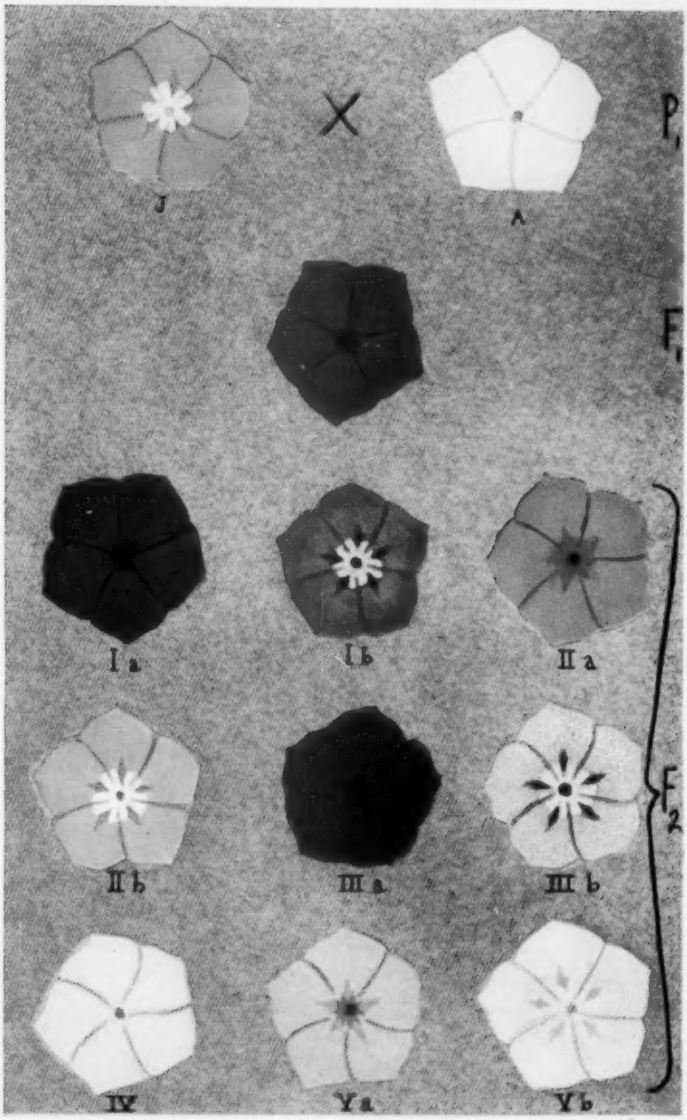
a. The white-eyed condition was recessive in the $F_1$ generation and reappeared in about one-fourth of the $F_2$ progeny; the white-eyed $F_2$ plants gave only white-eyed offspring in the $F_3$ generation.

b. The lightest-colored types, Va and Vb, constitute a minor system of colors independent of the rest of the color system, and present in cryptomeric condition probably with all the other colors; at least, one of the factors for the formation of this pale color appears so. Types Va and Vb are hypostatic to all the other color types and it is possible for all of them to throw Va and Vb, as shown in the $F_3$ results.

c. Unexpected and especially noteworthy is the fact that the main types, I, II, and III, apparently hold to each other the same relationship as do

LEGEND FOR PLATE 2

Types of flower color appearing in the JA series. Designated by J and A at the top are the parents that were crossed. Immediately below J and A is shown their $F_1$ hybrid; and below the latter the color types appearing in the $F_2$ and $F_3$ generations.


P
J
A
F1
I a
I b
II a
F2
II b
III a
III b
IV
V a
V b

the correspondingly designated types of the AB series and EF series. This means that the *non-stippled* (self-) magenta or Aster purple type,

TABLE 16

*Complete summary of data of $F_3$ families in the JA series.*

| $F_2$ parent, 1918 | | | $F_3$ progeny, 1919 | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| No. | Culture designation | Phenotype | Ia | Ib | IIa | IIb | IIIa | IIIb | IV | Va | Vb | Totals |
| 1 | $(JA)_{11.62}$ | Ia | 19 | 7 | 10 | 4 | 8 | 2 | — | 1 | 1 | 52 |
| 2 | $(JA)_{12.74}$ | Ia | 42 | — | 11 | — | 11 | — | 16 | — | — | 80 |
| 3 | $(JA)_{11.73}$ | Ia | 32 | — | 12 | — | 16 | — | — | — | — | 60 |
| 4 | $(JA)_{11.8}$ | Ia | 23 | 15 | 9 | 3 | 7 | 4 | — | — | 1 | 62 |
| 5 | $(JA)_{12.64}$ | Ia | 48 | — | — | — | 18 | — | 18 | — | — | 84 |
| 6 | $(JA)_{12.72}$ | Ia | 41 | 18 | 8 | 3 | 18 | 5 | — | 3 | 3 | 99 |
| 7 | $(JA)_{11.22}$ | Ib | — | 48 | — | 8 | — | — | — | — | — | 56 |
| 8 | $(AJ)_{102.8}$ | Ib | — | 33 | — | 4 | — | 7 | 12 | — | 1 | 57 |
| 9 | $(JA)_{11.36}$ | Ib | — | 22 | — | — | — | 7 | 9 | — | 1 | 39 |
| 10 | $(JA)_{11.15}$ | Ib | — | 15 | — | 8 | — | 6 | 20 | — | 2 | 51 |
| 11 | $(JA)_{11.5}$ | IIa | — | — | 4 | 1 | — | — | 6 | — | — | 11 |
| 12 | $(JA)_{11.16}$ | IIa | — | — | 22 | 11 | — | — | — | — | — | 33 |
| 13 | $(JA)_{12.56}$ | IIa | — | — | 19 | 6 | — | — | 13 | 4 | 3 | 45 |
| 14 | $(AJ)_{103.2}$ | IIa | — | — | 11 | 5 | — | — | 5 | — | — | 21 |
| 15 | $(JA)_{11.21}$ | IIa | — | — | 8 | 3 | — | — | — | 2 | 1 | 14 |
| 16 | $(JA)_{12.11}$ | IIa | — | — | 2 | 4 | — | — | 2 | — | — | 8 |
| 17 | $(JA)_{12.13}$ | IIa | — | — | 31 | 13 | — | — | 1 | 8 | — | 53 |
| 18 | $(JA)_{12.4}$ | IIa | — | — | 26 | 8 | — | — | 6 | — | — | 40 |
| 19 | $(JA)_{12.2}$ | IIb | — | — | — | 78 | — | — | 17 | — | — | 95 |
| 20 | $(JA)_{11.8}$ | IIb | — | — | — | 10 | — | — | 8 | — | — | 18 |
| 21 | $(JA)_{12.80}$ | IIb | — | — | — | 11 | — | — | 3 | — | 8 | 22 |
| 22 | $(JA)_{11.13}$ | IIIa | — | — | — | — | 31 | 12 | 11 | — | — | 54 |
| 23 | $(JA)_{11.19}$ | IIIa | — | — | — | — | 19 | 7 | 15 | 8 | 2 | 51 |
| 24 | $(JA)_{11.18}$ | IIIa | — | — | — | — | 28 | 8 | 12 | 5 | 2 | 55 |
| 25 | $(JA)_{11.80}$ | IIIa | — | — | — | — | 34 | — | 8 | — | — | 42 |
| 26 | $(JA)_{11.67}$ | IIIa | — | — | — | — | 39 | 15 | — | — | — | 54 |
| 27 | $(JA)_{12.42}$ | IIIb | — | — | — | — | — | 47 | — | — | 6 | 53 |
| 28 | $(JA)_{11.33}$ | IIIb | — | — | — | — | — | 15 | 7 | — | 1 | 23 |
| 29 | $(JA)_{12.81}$ | IIIb | — | — | — | — | — | 26 | 9 | — | 3 | 38 |
| 30 | $(JA)_{11.28}$ | Va | — | — | — | — | — | — | 8 | 20 | 11 | 39 |
| 31 | $(JA)_{11.50}$ | Va | — | — | — | — | — | — | — | 52 | 16 | 68 |
| 32 | $(JA)_{11.91}$ | Va(?) | — | — | 24 | 4 | — | — | 1 | 8 | 4 | 41 |
| | | | | | | | | | | | Total | 1518 |

IIIa, is equivalent to the *stippled* "dusky" type hitherto designated IIIa; a comparison was made of the living specimens of the JA and EF IIIa types and ignoring the stippled distribution of the latter, one would pronounce the two to be the same; it is interesting to note that the "b" mem-

ber of the III pair (distinguished especially by white eye instead of dark eye) shows its color more or less stippled. It should be said, too, that the type of EF duskies to which this JA type IIIa corresponds *is the more "reddish" of the "duskies";* it was not at all like the more "bluish" or violet member of the pair of EF "duskies"; the JA type III looks "blue" compared to its associates but we must evidently not attribute this condition to a bluing gene. In the JA series, also, type III never contains II, nor does type II contain III, as is evidenced by the experimental data in table 16. Type I contains both II and III, however, and is considered to be the interaction effects of these. These results were unexpected, since the color of type II of the JA series is in quality different from that of the AB and EF series.

With these observations in mind it is not difficult to construct a factorial scheme to interpret the results:

| A PARENT | J PARENT |
|---|---|
| *D*, same as in the AB and EF series. | *d*, absence or allelomorph of *D*. |
| *r*, absence or allelomorph of *R*. | *R*, factor for chromogen leading to the reddish pink anthocyanin of *J*. |
| *e*, absence or allelomorph of *E*. | *E*, factor for enzyme capable of converting chromogens into anthocyanin. |
| *M*, factor determining dark eye color; also an intensifier of blade color. | *m*, absence or allelomorph of *M*; in homozygous condition *m* determines the white-eyed condition. |

Table 17 lists the possible factorial combinations for this scheme, with the phenotype of each combination and the number of times it is expected to occur in every 256 individuals. The last column of table 15 lists alongside of the observed figures the numbers to be expected in every 217 individuals; a comparison of the observed and calculated numbers shows that the correspondence between theory and fact is fairly close.

TABLE 17

*The possible factor combinations for the $F_2$ generation of the JA series.*

| Factor combinations | Phenotypic formulae | Phenotype | Theoretical numbers |
|---|---|---|---|
| $E\,D\,R\,M$ | *EDRM* | Ia | 81 |
| $E\,D\,R\,m$ | *EDRm* | Ib | 27 |
| $E\,D\,r\,M$ | *EDrM* | IIIa | 27 |
| $E\,D\,r\,m$ | *EDrm* | IIIb | 9 |
| $E\,d\,R\,M$ | *EdRM* | IIa | 27 |
| $E\,d\,R\,m$ | *EdRm* | IIb | 9 |
| $E\,d\,r\,M$ | *EdrM* | Va | 9 |
| $E\,d\,r\,m$ | *Edrm* | Vb | 3 |
| $e\,D\,R\,M$ | *eDRM* | IV | 27 |
| $e\,D\,R\,m$ | *eDRm* | IV | 9 |
| $e\,D\,r\,M$ | *eDrM* | IV | 9 |
| $e\,D\,r\,m$ | *eDrm* | IV | 3 |
| $e\,d\,R\,M$ | *edRM* | IV | 9 |
| $e\,d\,R\,m$ | *edRm* | IV | 3 |
| $e\,d\,r\,M$ | *edrM* | IV | 3 |
| $e\,d\,r\,m$ | *edrm* | IV | 1 |
| | | Total | 256 |

GILBERT (1915) briefly described the results of three hybridizations in *Phlox Drummondii* in all of which a variety called "Carnea" was the pollen parent. From the colored plate accompanying his article it is obvious that his "Carnea" is like the J strain of my cultures; his seed parents were different, none of them bearing completely white flowers. One of his crossings gave $F_2$ results that make interesting comparison with the JA data presented above. He crossed his "Carnea" to a variety he says was known commercially as "Coccinea." This is described and pictured as bluish lilac with a dark eye. His plate D shows it to closely resemble the type IIIa ("dusky") already described. His $F_1$ flowers were what would be expected if my J or type IIb and "dusky" were crossed, i.e., a brilliant carmine, and resembling the $F_1$ in my JA series. GILBERT's $F_2$ generation of 115 plants comprised seven types; his plate would seem to prove that five of these types closely corresponded to or were identical with the types Ia, Ib, IIa, IIb, and IIIa of this paper. A sixth type with formula in the text including factors *"ee"* (= white eye) and *described as white,* was *pictured* as a dark-eyed white. His seventh type is described and pictured as a dark-eyed white and was reported once in the 115 plants. Assuming that his sixth type was as his text described, GILBERT secured six of the nine types which are here re-

ported for the JA series. The total absence in GILBERT's cultures of a type like IIIb is surprising as is also the fact that the faintly colored independent types were not reported.

To interpret these results GILBERT supposed three factors necessary (with their recessive allelomorphs), (1) a factor for dark eye, (2) a factor for blue pigment, and (3) a distinct and independent "red" factor carried by the "Carnea" (= J) parent; these factors, in general, correspond to the writer's *M, D,* and *P,* respectively. GILBERT did not expressly state that the bright carmine was an interaction product of the factors for his dusky and reddish-pink sorts, but his genetic formulae imply this.

| | | |
|---|---|---|
| Bright carmine, | *EEBBRR* | (corresponds to my type Ia) |
| Reddish-pink, | *EEbbRR* | ( " " " " IIa) |
| Bluish-lilac, | *EEBBrr* | ( " " " " IIIa) |

GILBERT carried none of his crosses to the $F_2$ generation so that he could not know from actual breeding that his reddish-pink never carried the gene for bluish-lilac, nor that the bluish-lilac never threw the reddish-pink, and that the heterozygous carmines could give both in the next generation thus pointing to the reddish-pink and bluish-lilac as resolution products.

In another of GILBERT's crosses, he records an unexpected *preponderance of white* "which is unaccounted for." An explanation of this condition has been presented above in the exposition of the results of the AB series.

## SOME SIMPLER CASES OF COLOR INHERITANCE IN PHLOX DRUMMONDII

### *The crossing of white-eyed tyrian rose (P) and white-eyed pink (J)*

The line to which the P parent belonged has been carried on in pedigree culture in small numbers from season to season. No deviations from type have been noticed. In this P strain the flowers are white-eyed with outer blade about a brilliant tyrian rose. The J type has already been described and pictured. The two individuals used as parents were crossed reciprocally giving seed for an $F_1$ generation of 12 plants; the flowers of the $F_1$ generation were all indistinguishable from those of the inbred P strain.

Three of the $F_1$ plants furnished seed for an $F_2$ generation of 218 plants grown in 1918. The $F_2$ group presented a sharp segregation into

the two parental types, there having been 165 P type to 53 J type. On a simple unifactorial basis expectation calls for 163.5 P type to 54.5 J type. The correspondence, therefore, is very close.

By the conventional manner of Mendelian interpretation these experimental results would lead to the statement, probably, that we have obtained a definite idea of the specific difference between P and J, that a factor in the J parent conditioning the reddish-pink J coloration is allelomorphic to a different factor in the P parent making for the carmine color. It would seem that the matter is not so simple as it appears, however. The segregation, of course, indicates a difference of some kind, but gives us no idea of the nature of the difference. The evidence on which this assertion is based was secured in the JA series; the P type really arose there anew following hybridization and recombination and was designated as type Ib. The P strain was like the slightly darker variants of type Ib in the JA series. We learned there that Ib (and, hence, supposedly, P) is due to the composite or complementary effects of the factors for J (= IIb) and for the stippled mallow pink (= IIIb); that is P = J (IIb) + IIIb. We inferred also that J never carries IIIb; and that the types that correspond to P and J *both* carry the gene for the J pigmentation. The hybrid between P and J must have been, therefore, homozygous for the factor conditioning J, and the segregation of J in 25 percent of the $F_2$ in this JP series does not point to the real difference between J and P. The real difference between P and J, which is the presence of the complementary gene for mallow coloration, i.e., for type IIIb (present in P and lacking in J), we know from our previous results in the JA series, but would probably have never even suspected from the results of crossing J and P. All gametes of the $F_1$ generation (in the JP series), then, contained the factors for producing the J type of color; half of these in addition held the factor for the IIIb type of coloration revealed in the JA series and half lacked the latter; all $F_2$ zygotes of the P type must have carried the gene for IIIb color and all J zygotes presumably lacked this factor. We arrive thus at a seemingly paradoxical position: the 53 J segregates of the $F_2$ generation indicated a feature in which the parents were similar and the real difference was masked, for wherever the really differentiating factor for the mallow pink color appeared it was compelled to give a full-colored interaction product, because of the homozygous condition of the factor for the J color; and the absence or allelomorph of this factor for mallow-pink would allow the unchanged J color to appear.

The results of crossing P and J, therefore, pointed to a unifactorial difference but, in themselves, really furnished no clue as to the real nature of the difference.

*The genetic relationship of white (A) and cream (F)*

Both parents were from pedigree lines grown in considerable numbers during several seasons and were known to be breeding true—the former, strain A, for completely white flowers, and the latter, strain F, for completely cream-colored flowers. Various members of the two types or strains were crossed giving seed for an $F_1$ generation of 47 plants; all $F_1$ hybrids were completely white and indistinguishable from the A parent. Reciprocal hybrids were included but the $F_1$ plants were white no matter whether the seed parent was white or cream.

Seven of the $F_1$ individuals provided seed for an $F_2$ generation of 169 plants; the group presented a simple segregation into 132 white and 37 cream. The expectation for a monomeric difference in the case of 169 individuals is 126.75 : 42.25. The fit of the theoretical to the actual is close enough to warrant postulating a single factorial difference operating to distinguish the white from the cream.

*The genetic relationship of white with dark eye (B) and cream without dark eye (F)*

Various individuals of both types were crossed reciprocally. The parents were from lines which have been for several seasons in pedigree culture and known to be true to their respective types. Reciprocal hybrids were identical. A total of 67 $F_1$ hybrids bloomed during 1917 and 1918, and all were similar, bearing white flowers with dark eyes, resembling the B parents.

Several $F_1$ plants gave seed for an $F_2$ generation of 213 individuals. Four sharply distinct types appeared among these $F_2$ plants, the types and their numbers being given in table 18.

TABLE 18

*Actual and theoretical composition of the $F_2$ generaton from the cross of B and F.*

| $F_2$ types | Observed numbers | Calculated numbers |
|---|---|---|
| Dark-eyed white | 112 | 119.8 |
| Dark-eyed cream | 37 | 39.9 |
| Completely white | 47 | 39.9 |
| Completely cream | 17 | 13.3 |
| Total | 213 | 212.9 |

Obviously two independent factorial differences are at work in this case, the factor *W*, a dominant one, determining the white color of the plastids; its allelomorph, *w*, when homozygous, causes the cream color of the plastids. The other factor has already been encountered in the JA series, i.e., *M*, which causes the appearance of an anthocyanin eye at the centre of the flower; its allelomorph, *m*, is responsible for the colorless condition at the centre. In the last column of the table the expectations on such a basis are entered.

## CONCLUSIONS AND SUMMARY

1. Since the introduction of *Phlox Drummondii* into culture less than 85 years ago a large number of marked variations has occurred, offering good opportunities for the genetical analysis of the species.

2. The distinguishing features of the several varieties upon which the present report is based, and their cultural designations (not to be confused with the factorial symbols) are as follows:

| | |
|---|---|
| Cuspidate flowers | L |
| Funnel-shaped flowers | I |
| Completely white flowers | A |
| Dark-eyed white flowers | B |
| Dark-eyed brilliant carmine or pomegranate purple flowers | E |
| Completely cream flowers | F |
| White-eyed reddish pink | J |
| White-eyed tyrian rose | P |

3. An hereditary variation named var. *cuspidata* has arisen with much reduced corolla limb bearing on each lobe of the corolla two short lateral teeth and one long median tooth. A difference of a single gene distinguishes the entire-petalled from this cuspidate-petalled kind. An independent factor or factors (for breadth of lobes) interacts with the *cuspidata* and alters the character of the side teeth.

The *fimbriata* "variety" is merely a simple monoheterozygote of the entire and *cuspidata* types; it represents the only case of non-dominance for a factor, thus far known in *Phlox Drummondii*. The hybrid nature of *fimbriata* necessitates certain taxonomic amendments, indicated in the presentation.

The *cuspidata* gene would seem to act (chiefly) to decrease the rate of epidermal growth, this inhibition being weaker in three locations. The factorial symbol $I_e$ is suggested to designate this factor.

4. Another hereditary variation in the form of the flower is represented by the funnel-shaped phloxes; a single factorial difference distinguishes the funnel-shaped from the salver-shaped condition normal for the Phlox genus. The factor *S* is presumed to determine the salver shape and its allelomorph *s*, which is completely recessive, the funnel shape. Two other grades of corolla expansion were found. The factor *s* itself or some other uninvestigated gene closely linked with it, causes the colored funnel-shaped flowers to appear white-streaked.

5. There are pairs or sets of complementary factors in *Phlox Drummondii*. In some cases in addition to the compound or interacting effect, the individual members of the pairs or sets are capable of separate and distinct somatic expression. In other cases each pair or set of genes becomes evident only in the single compound character, the components remaining latent (invisible or cryptomeric) when not present together.

a. The crossing of the strains A and B (in both of which the flower blades are white) and of A and J (the former with white blade and the latter with light pink) gave in each case a surprisingly different full-colored $F_1$ type.

b. The simultaneous presence of three factors is necessary before a simple blade color can develop; the $F_1$ hybrid of A and B proved heterozygous for all three of these necessary factors as evidenced by the large proportion of $F_2$ white-bladed plants and the character of the families from $F_2$ colored plants. The three factors are conceived to be, first, one, *P*, that leads to chromogen formation; secondly, one *E*, that leads to the production of an enzyme; and lastly one that leads to the production of an activator of the enzyme, *A*.

c. The simple type of blade color caused by the presence of the minimum complement of the three necessary factors varies, depending presumably on the character of the chromogen base present. One (type IIb of the AB and EF series) is thought to be due to the simultaneous presence of genes *E* and *A*, and the chromogen-producing gene *P*. A second simple type of blade color, the "dusky," both stippled and unstippled, is supposed to be due to the same factors, *E* and *A*, acting on a different chromogen due to the factor *D*. A third of the simple types is considered due to the factors *E* and *A* acting on a chromogen *R*.

d. The $F_2$ and $F_3$ data led to the following inferences: Blade color type due to *P E A* + type due to *D E A* = a distinct full-colored type designated Ia in the account of the AB and EF series and in plate 1. Ia is

considered to be due merely to the interaction of factors *P* and *D* in the presence of *E* and *A;* no factors that may be called specific for the Ia type are in play. Similarly, the type due to factors *R E A* + the type due to *D E A* give a full-colored type designated Ia in the JA series and in plate 2. These generalizations are based on the character of the $F_3$ results; the critical test, the actual putting together of the simple types by hybridization has not been accomplished.

6. Modifying factors have been in evidence:

a. The AB and EF series of plants exhibited a bluing factor (or linked pair of factors(?)), independent of the essential color producers, which doubled the number of the color groups; for every "reddish" group it made a corresponding more "bluish" group.

b. A simple dominant diluting factor of minor effect occurred in the EF series,—designated $D_i$.

c. A minor factor, slightly reddening and intensifying simultaneously was referred to briefly in the EF series,—designated $D_e$.

d. The dark-eye factor, *M,* led to intensification of the blade color.

7. Dark-eyed forms differ from the light-eyed forms by a single factorial difference,—designated *M*. Its allelomorph causes the white eye.

8. The cream-colored condition is a simple recessive to the white-colored; gene *W* determines whiteness and its allelomorph, *w,* causes the cream. The same relationship of white to cream is inferred from GILBERT's published results.

9. The chromosome number in *Phlox Drummondii* is 14 for the cells of the root-tip.

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